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A Partial Differential Equation Model of Fish Population Dynamics and Its Application in Impingement Impact Analysis

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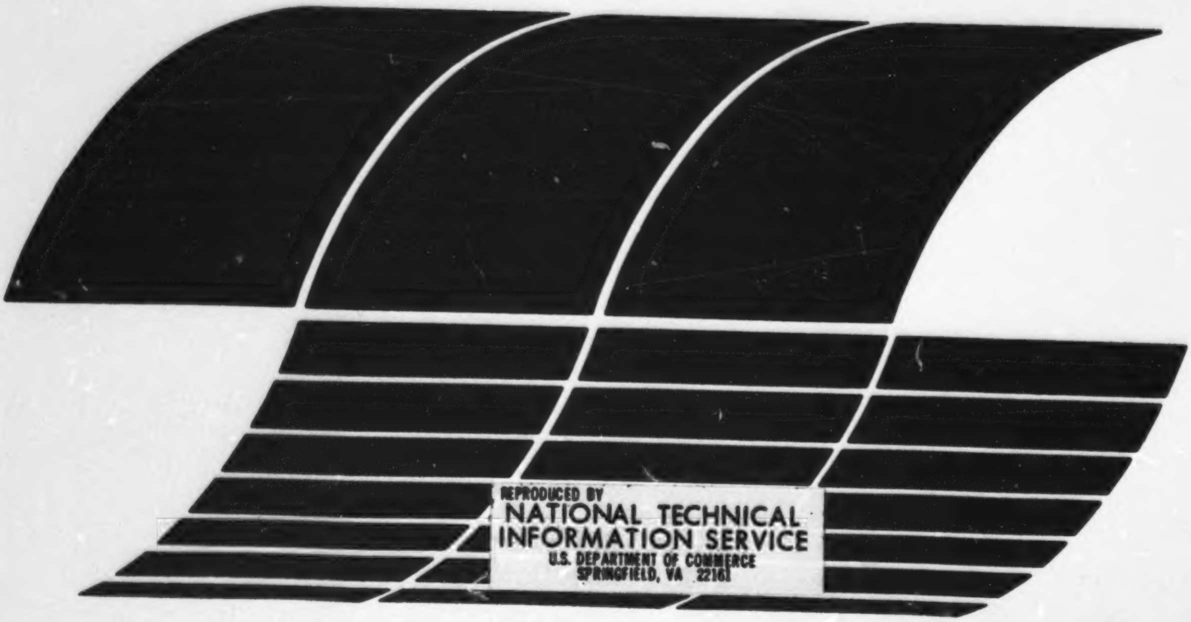

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The report gives results of a study to: (1) develop a mathematical model describing fish populations as a function of life process dynamics and facilities that impose additional mortality on fish populations; and (2) improve objective impingement impact prediction. The model accounts for hatching, growing, and mortality as functions of time and permits computer simulation of impingement impact. It also accounts for the genetic and environmental heterogeneity effects on the growth of a cohort of fish. Gizzard shad data collected by TVA were used to corroborate the model. Simulated impingement impacts for the steam-electric generating plant reservoir studied were much less than could be measured in field studies. For a tenfold increase over observed impingement losses, the model predicted that gizzard shad stock levels would fall by < 10% for any age group. Similarly, the model with a hundredfold increase over the observed losses predicted that age IV gizzard shad stock levels were reduced about 65% from baseline values, with younger groups showing less response. Model simulations revealed that intake-induced mortality reduced the total numbers of gizzard shad in each age class by < 1%. These findings show little effect for a species having high natural mortality, but they cannot be generalized to other species with significantly different natural mortality patterns.

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ABSTRACT

This study was undertaken to (1) develop a model describing fish populations as a function of life process dynamics and facilities which impose additional mortality on fish and (2) improve objective impingement impact prediction. The mathematical model developed accounts for hatching, growth, and mortality as functions of time and permits computer simulation of impingement impact. It also accounts for the genetic and environmental heterogeneity effects on the growth of a cohort of fish. Gizzard shad data collected by TVA were used to corroborate the model.

Simulated impingement impacts for the steam-electric generating plant and reservoir studied were much less than could be measured in field studies. For a 10-fold increase over observed impingement losses, the model predicted that gizzard shad stock levels would fall by less than 10 percent for any age group. Similarly, the model with a 100-fold increase over the observed losses, predicted that age IV gizzard shad stock levels were reduced about 65 percent from baseline values, with younger age groups showing less response. Model simulations revealed that current levels of intake-induced mortality reduced the total numbers of gizzard shad in each age class by less than 1 percent. These findings show little effect to a species having high natural mortality, but cannot be generalized to other species having significantly different natural mortality patterns.

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LIST OF ABBREVIATIONS AND SYMBOLS

ABBREVIATIONS

cm -- centimeters
ha -- hectares
kg -- kilograms
m -- meters
MWe -- megawatt electrical
mg -- milligrams
mm -- millimeters

SYMBOLS

$B(s,t)$ -- fecundity going into size class s
$B_0(t)$ -- fecundity, all going into size class s_0
Δs -- increment in size
Δt -- increment in time
$G(s,t)$ -- growth rate as a function of size and time
$G(s)$ -- growth rate, assumed dependent only on size
g_0 -- growth rate constant
$I(s_0,s)$ -- integral, defined in Eq. (A.23)
$J(s_0,s)$ -- integral, defined in Eq. (A.24)
$N(s,t)$ -- size distribution function
N_t -- number of fish at start of year
N_{t+1} -- number of fish at end of year
$N_{o_{t+1}}$ -- number of young-of-the-year fish at end of year
S_R -- scale radius
s -- size
s_0 -- minimum size of fish in the cohort
s_{max} -- maximum size of fish in the cohort
t -- time
TL -- total length
T_s -- length of spawning period
$Z(s,t)$ -- mortality rate coefficinet as a function of size and time
$Z(s)$ -- mortality rate, assumed dependent only on size

Z_0 -- constant mortality rate

$Z_f(s,t)$ -- fishing mortality rate coefficient

$Z_n(s,t)$ -- natural mortality rate coefficient

SECTION 1

INTRODUCTION

Section 316(b) of the Clean Water Act has focused much attention on the impingement of fish on water intake screens at power plants. Although well documented, impingement is a poorly understood phenomenon. In many instances, the species and sizes of fish affected are known to have swimming speeds sufficiently greater than needed to avoid entrapment. While it is frequently possible to relate unusually heavy impingement of some species to cold shock, heavy losses of cold tolerant species (or cold sensitive species during periods of warm water temperatures) continue to puzzle investigators.

It is interesting to note that trawls fished for commercial fish stocks are generally towed at speeds well below either burst or sustainable swimming velocities of the target species. Therefore, as a first step in attempting to understand the impingement phenomenon, it may be productive to think of water intake screens as "stationary trawls." Water is pulled through this "stationary trawl" rather than the trawl being pulled through the water. Indeed, intake screen "catches" have been compared to conventional trawl catches in order to gain some perspective of the magnitude of impingement losses.

Assessments required by Section 316(b) of environmental impacts owing to impingement have taken many forms. In some cases, although no attempt was made to relate impingement mortality to the affected population, it was the opinion of the investigator(s) that estimated impingement losses were not an adverse impact to the fish community (Duke Power Company, Undated). Other investigations have related impingement losses to estimated standing stocks in the affected water body, and while noting that some fraction of the stock was killed, similarly opined that such losses did not constitute an adverse impact (Commonwealth Edison Company, 1977).

Another approach (Tennessee Valley Authority, 1977a) translated impingement losses into reservoir area of lost production (i.e., for an estimated standing stock of 10,000 fish/ha coupled with impingement of 2,000,000 fish annually, a loss of 200 ha of production is predicted. For a 20,000-ha reservoir, this is 1 percent of the total area). A fourth approach compared impingement losses with commercial catch for a given species (Moseley, et al., 1975). Since numbers of impinged fish are always much less than the commercial catch, impact is presumed to be small or negligible. Although most of these "impact assessment" techniques put impingement losses into at least a reasonable perspective, none truly addresses impact; i.e., the actual or predicted modification of fish communities by an extraneous mortality source.

In the case of new or proposed facilities which take in considerable volumes of water, preoperational studies of the near- (and/or far-) field fish community can be compared to similar studies during the operational phase of the facility. Although this approach would appear ideal for determining the impact of such a facility to the resident fish community, it is fought with uncertainty. Documented changes in the far-field fish community during an extended study period may not necessarily be due to plant operation since changes through time are frequently observed in waters where facilities do not exist (Tennessee Valley Authority, 1978). Additionally, sampling techniques may not be sufficiently sensitive to reliably determine subtle far-field impacts.

While determination of impacts in the above situation seems tenuous at best, in the case of existing facilities for which preoperational data are unavailable, criteria for assessing operational impacts to the far-field fish community are even more obscure. The use of documented changes during a protracted study period is obviously subject to the earlier given criticisms for such an approach. It is clear that the existing fish community "is what it is" under the operating regime of the water intake facility. What is not clear is what the far-field fish community in question would be in absence of the plant.

If observable adverse modifications of fish communities cannot reasonably be coupled with cause-effect relationships owing to plant operation, or if the fish community was not studied prior to operation of the facility, the investigator is reduced to two approaches: (1) offering an "expert" opinion as to probable impact, or (2) modeling the fish community (or population) and the effect of plant operation on it.

It is in this latter vein that this project was undertaken. A model which describes fish populations in terms of both life process dynamics and their interaction with facilities which impose additional mortality is much needed. The purpose of this task was 2-fold: (1) to develop such a model, and (2) to remove as much of the subjective process of impingement impact prediction as possible.

SECTION 2

CONCLUSIONS

The parameters needed by the model were estimated from data of a gizzard shad population in Barkley Reservoir. The model was then used to simulate the total population and length distribution under (1) baseline or current conditions, (2) the use of assumed zero plant mortality, (3) a 10-fold increase in plant mortality, and (4) a 100-fold increase in plant mortality.

The model proved to be effective in simulating the observed total population numbers, though its predictions of the length distributions were narrower than those of the observed population. Model simulations indicated that present plant-induced mortality lowers total numbers in each age class by less than 1 percent. A 10-fold increase in plant mortality is predicted to cause at worst a 10-percent decrease of age class IV. A 100-fold increase in plant mortality would have significant effects according to the model, lowering the number of fish in age class IV by about 65 percent.

Apparently, the gizzard shad population in Barkley Reservoir is virtually unaffected by impingement at current levels. However, these results cannot be generalized to other species which do not possess great compensatory powers.

SECTION 3

RECOMMENDATIONS

The unexpectedly low impingement impacts predicted for gizzard shad in Barkley Reservoir were at least in part due to the compensatory powers possessed by this species. Relatively short lifespan, density dependent growth, and high natural mortality all contributed to greatly reduce the effects of impingement losses for this species in Barkley Reservoir. Therefore, these results probably cannot be generalized to other species and the model should be tested with a relatively long-lived species which does not typically possess great compensatory powers.

Model predictions for impingement impact levels approximating those in both cooling ponds and rivers where virtually the total flow is entrained should be compared with actual data from such situations. This would provide a valid test of the model's predictive abilities. Should relatively great modifications be required to achieve accurate predictions, they could well lead to new approaches in modeling the field of fish population dynamics.

The model is more flexible and has greater capabilities than were used in this study. It could be used to predict the total impact of intake-related mortalities (entrainment as well as impingement) since the model permits inclusion of all sizes and ages of fish if data are available. Therefore, it is recommended that the model be tested using all sizes of a particular fish species affected by intakes.

SECTION 4

MATERIALS AND METHODS

THE MODEL

All of the individuals of a particular fish species in a given body of water collectively form a unit termed a population. These individuals undergo three distinct processes: birth, growth, and death. Although these processes are properties of individuals, taken collectively they form the basis for what is known as dynamics of the population.

Birth

Virtually every current fish population model assumes that all individuals of a cohort are born (or hatch) at the same time. This obviously simplifies the determination of age, growth, and mortality rates through time. However, hatching typically occurs over a period of time as depicted in Figure 1. The essential elements of this figure are the time when hatching begins, builds to a peak, declines, and finally ceases. This period of hatching may be from a few days to several months in length, depending upon the species in question. In the latter instance, the simplifying assumption that all hatch on the same day is not only unwarranted, it is in serious error.

Returning to Figure 1, note that all members of a cohort are shown in this graph, and as such the collective property (birth or hatching) depicted becomes a population process. This graph is actually a 3-variate or 3-dimensional figure of numbers through time for which the third variable, size, is fixed. In this case, the "fixed size" is length at hatching. It could just as easily have been "fixed" for some other length of "significance"; i.e., the length(s) at which a cohort becomes vulnerable to impingement. However, the choice of length at hatching has two particularly important attributes. The area beneath the curve in Figure 1 is the total number hatched. This is determined by integrating an equation describing this curve and the slope of this integral form is the hatching rate.

The concepts of three dimensionality and fixing of one variable are important as they will form the basis for mathematical description of the model developed in this report.

Growth

As mentioned previously, growth is a property of individuals. When growth is considered collectively for a cohort, it becomes a cohort or population process.

Figure 2 is a commonly used graphic representation of cohort length-frequency. Numbers and length are seen to vary for a "fixed" or particular instant in time. Although the members of the cohort are all in the same year of life, they are not of exactly the same age as noted earlier. While the scatter of observed lengths is in part due to differences in age

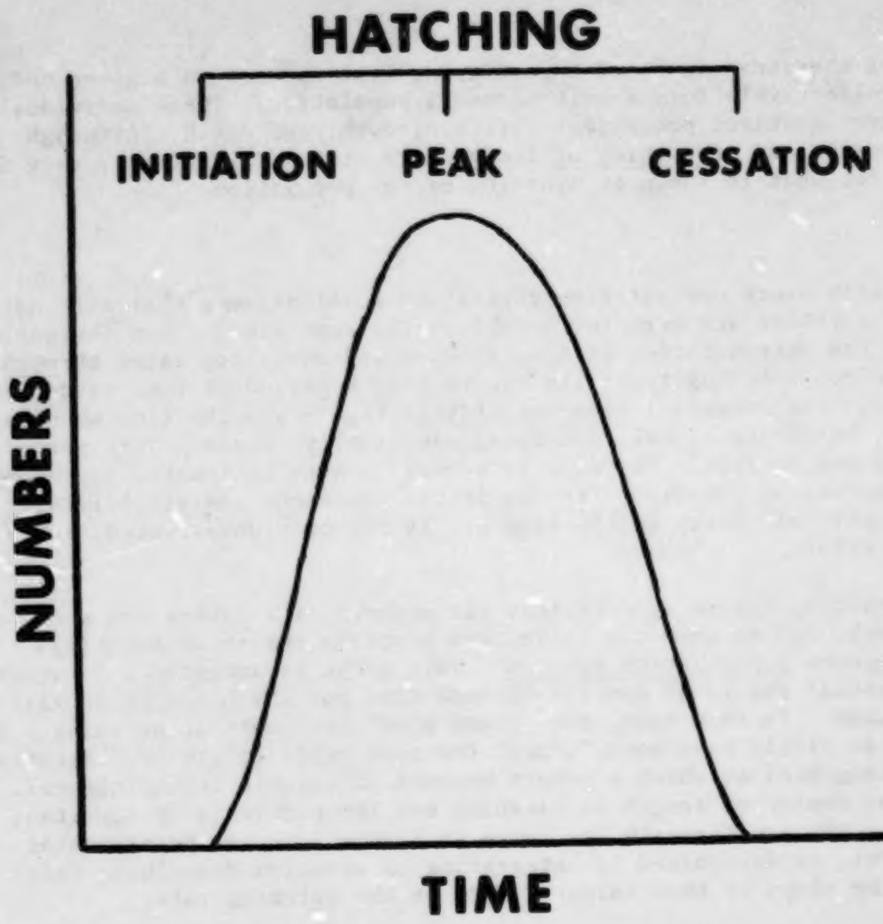


Figure 1. The hatching of a cohort of fish through time (the reproduction season).

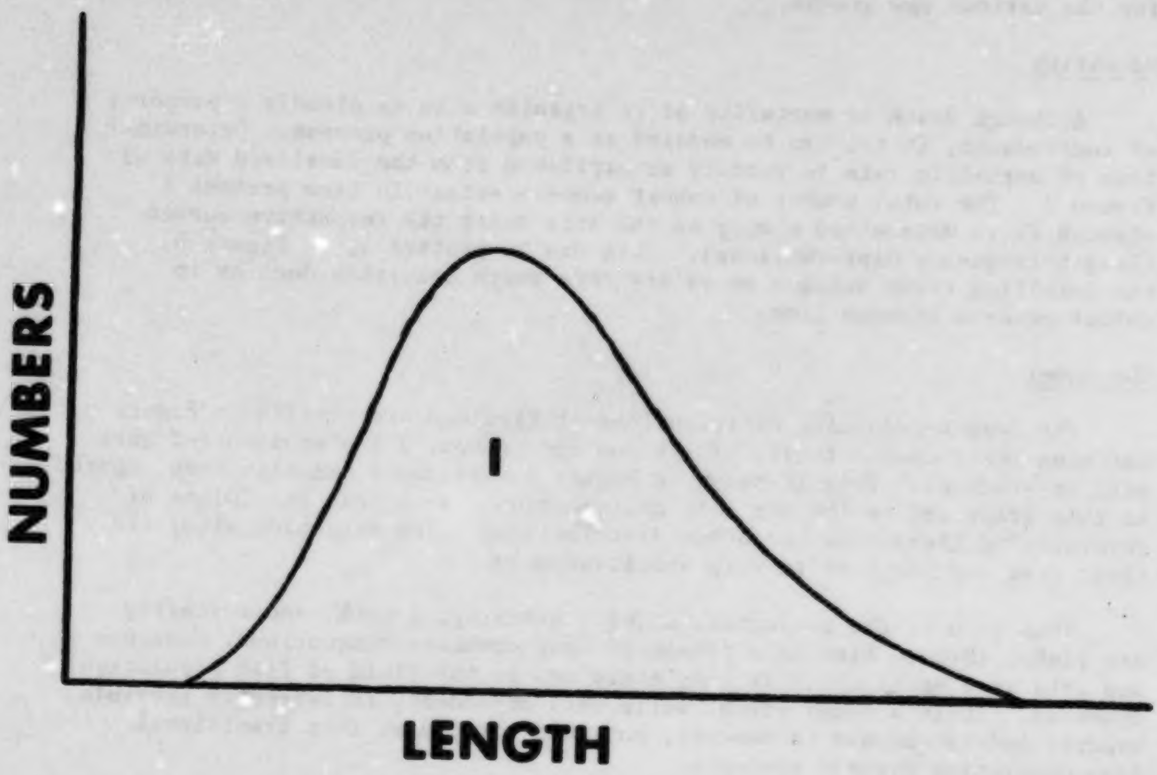


Figure 2. A cohort of fish at a given instant in time.

(thus a longer period of growth), differential growth of individuals is also a factor. The positive skew is a typical pattern although others, such as biomodality, occur.

If a cohort is followed through time, the pattern shown in Figure 3 will typically emerge. Here time is effectively "fixed," at several points to study growth. A more common graphical representation of this phenomenon is shown in Figure 4. In this instance numbers are "fixed." The scatter of lengths in Figure 4 is the same as that for the respective groups in Figure 3. Growth is simply determined in Figure 4 as the average length for the various age groups.

Mortality

Although death or mortality of an organism also is clearly a property of individuals, it too can be modeled as a population process. Determination of mortality rate is readily accomplished from the idealized data of Figure 3. The total number of cohort members extant in time periods I through IV is determined simply as the area under the respective curves (length-frequency distributions). This can be plotted as in Figure 5, the resulting curve being a mortality rate which describes decline in cohort numbers through time.

The Model

The length-frequency distributions of Figure 3 are erected on Figure 4, matching their common length ranges and age groups, a 3-dimensional figure will be produced. This is shown in Figure 6. Figure 1 has also been imposed on this graph and is the far left distribution. Note that its "plane of reference" differs from the other distributions. The variables along the three axes are now free to vary simultaneously.

This then is the conceptual model. Hatching, growth, and mortality are linked through time in a framework that combines conventional concepts and data in a model which is completely new to the field of fish population dynamics. It is a model which, while data dependent, is extremely flexible, readily understandable in concept, and does not depart from traditional fish population dynamic concepts.

To be useful, the model must be quantitative as opposed to the dimensionless values used to develop it up to this point. This will require the mathematical description developed in subsequent sections.

MATHEMATICAL DESCRIPTION OF THE CONCEPTUAL MODEL

Formulation of a partial differential equation model

Partial differential equations were probably first applied to population dynamics by von Foerster (1958). Such equations are useful in describing a population through time, not only in terms of numbers of individuals, but also age or size distributions of the population. Description of length distributions is especially important since most fisheries are concerned with fish numbers and sizes. Also, the inclusion of age or size

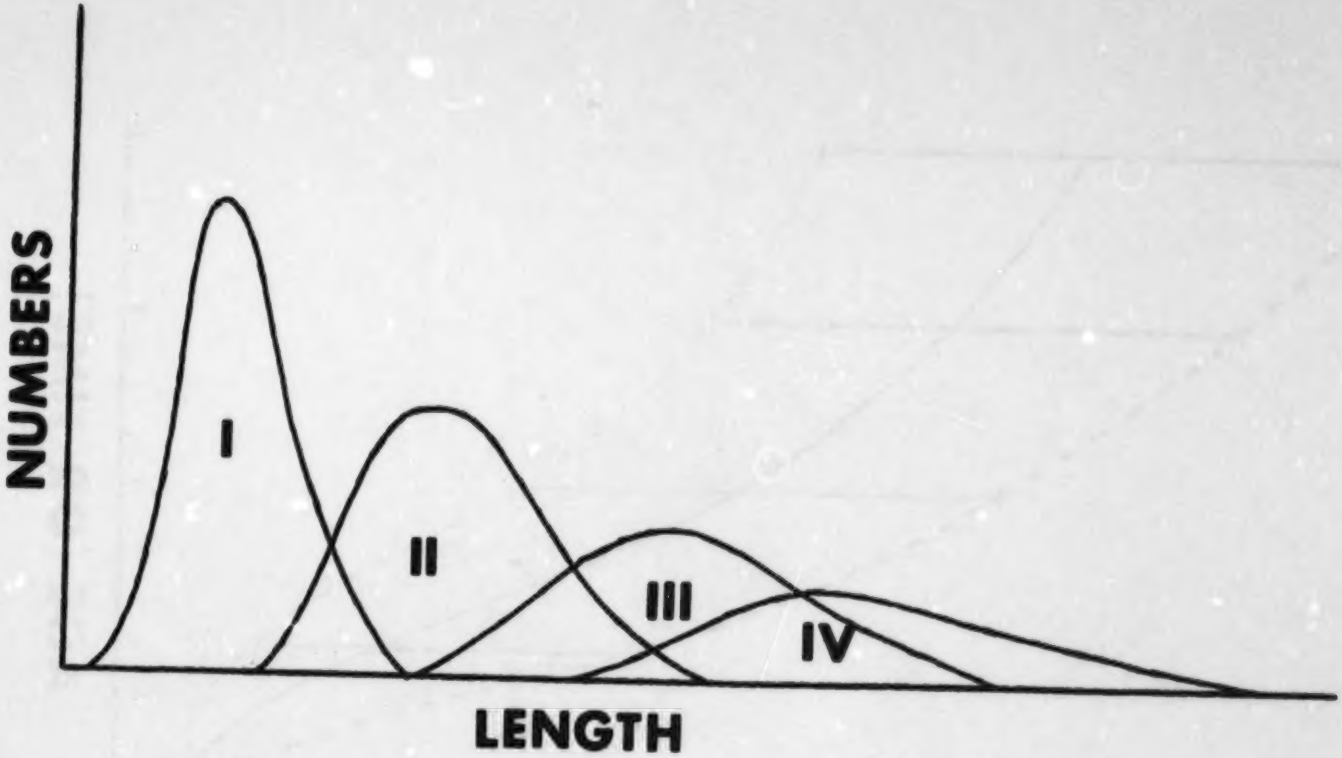


Figure 3. The same cohort of fish in Figure 2 shown at four instances in time.

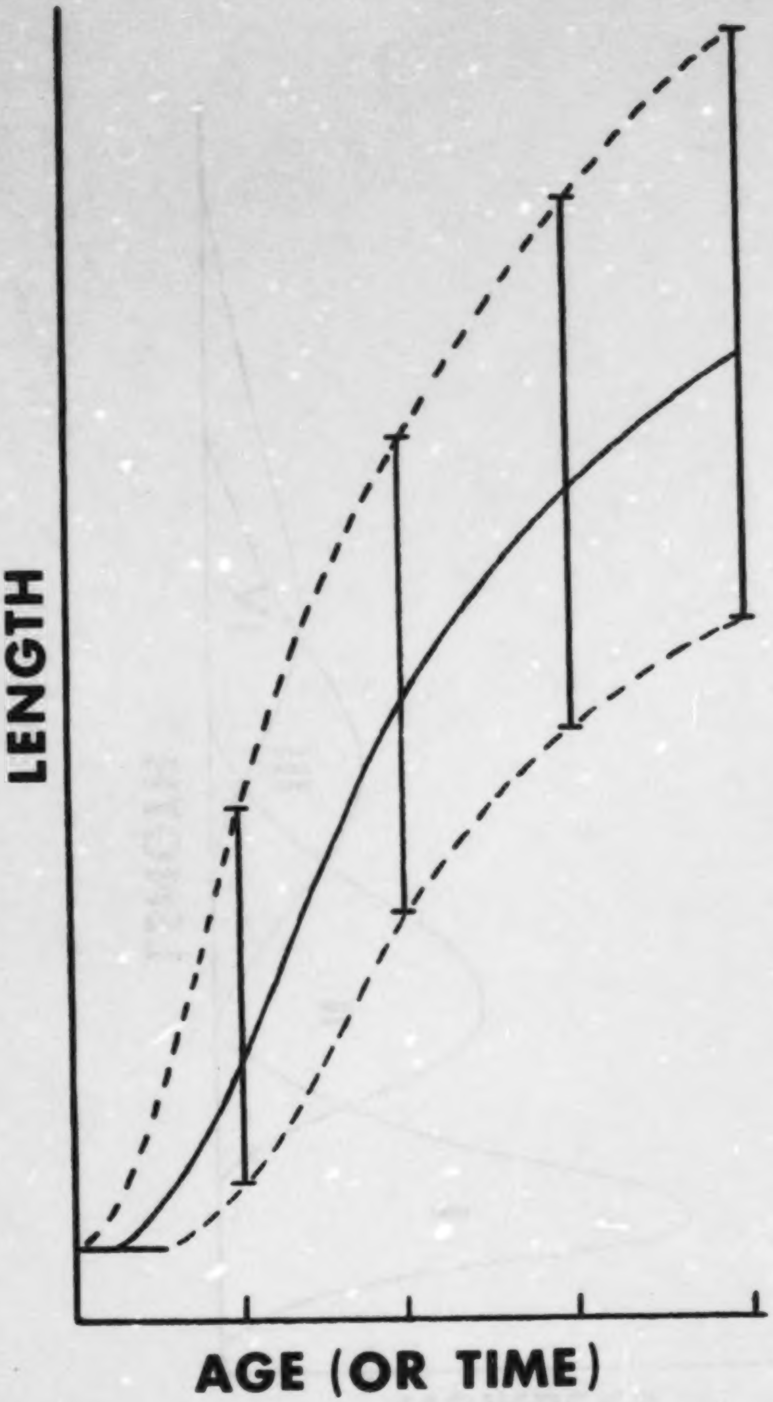


Figure 4. Graphic representation of the cohort of fish in Figure 3 to better show growth.

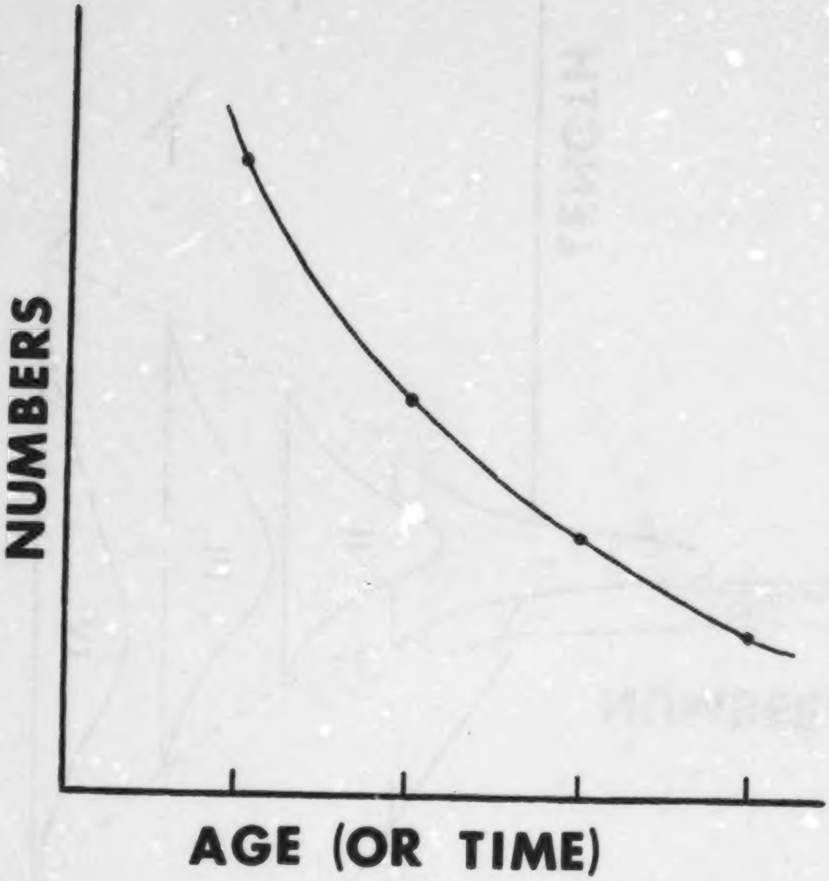


Figure 5. Mortality in a cohort of fish.

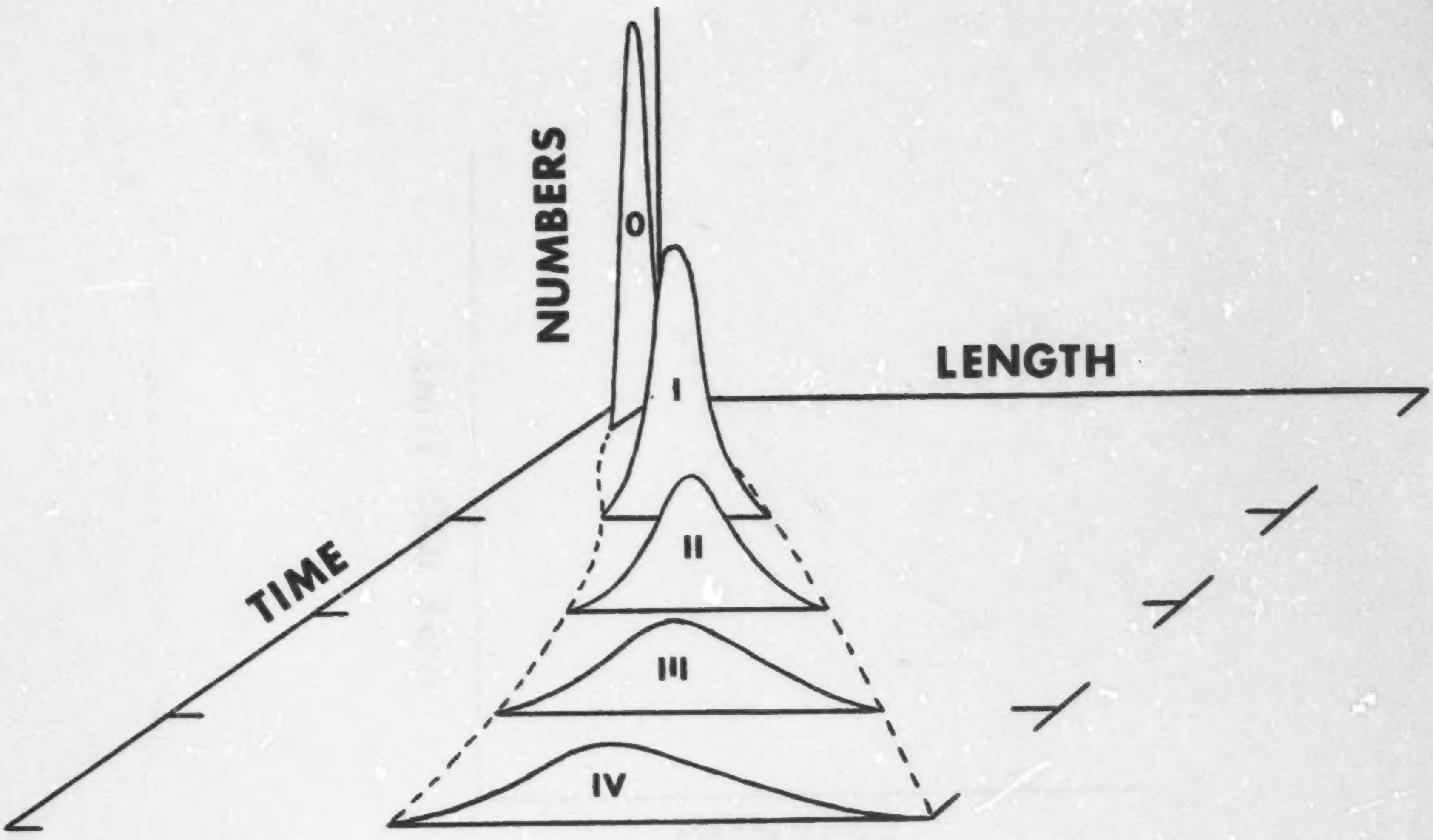

NUMBERS
LENGTH
TIME
0
I
II
III
IV

Figure 6. Relationship of hatching, growth, and mortality in a cohort of fish.

structure implies a time-lag effect in the population, essential in properly describing the dynamics. Partial differential equation models have been used to describe the age and size structures of populations by Trucco (1965a,b), Oldfield (1966), Weiss (1968), Sinko and Streifer (1967, 1971), Langhaar (1972), Oster and Takahashi (1974), Rubinow (1973), Rotenberg (1975), Griffel (1976), and Van Sickle (1977), among others.

Before developing the model, two population characteristics of interest are described, mortality and growth of the individual fish.

The rate of growth of an organism can often be approximated by the differential equation

$$\frac{ds(t)}{dt} = G(s(t),t) \ , \tag{1}$$

where s(t) is some measure of organism size (e.g, length) as a function of time, and G(s,t) is a function of both size and time. When G(s,t) takes some simple functional form, independent of t, for example,

$$G(s) = g_0(1 - \frac{s}{s_{max}})s \ , \tag{2}$$

where g_0 and s_{max} are constants, then Eq. (1) yields the solution,

$$s(t) = \frac{s_0 s_{max} e^{g_0(t - t_0)}}{(s_{max} - s_0) + s_0 e^{g_0(t - t_0)}} \tag{3}$$

where t_0 is some initial time and s_0 is the initial size.

The mortality of fish in a single cohort is typically modeled as,

$$\frac{dN(t)}{dt} = -Z\{s(t),t\}N(t) \ , \tag{4}$$

where N(t) is the number of organisms and Z{s(t),t} is a mortality function, in general dependent on both time and the average size of organisms in the cohort. For simple cases, Eq. (4) is easily solved. For example, if Z{s(t),t} is merely a constant, Z_0, then

$$N(t) = N_0 e^{-Z_0(t - t_0)} \tag{5}$$

where NO is the number in the cohort at time to.

Size distribution, N(s,t), means the number of organisms per unit size class at a given time. An equation will be derived to describe the change in N(s,t) through time. Consider, at time t, the number of organisms in a size class of width Δs centered around the size s, and denote this number by N(s,t) (see Fig. 7). Assume a very short interval of time, Δt, passes. What is the new distribution at t + Δt? Conceptually, the number of fish in size class s and time t + Δt can be symbolized as

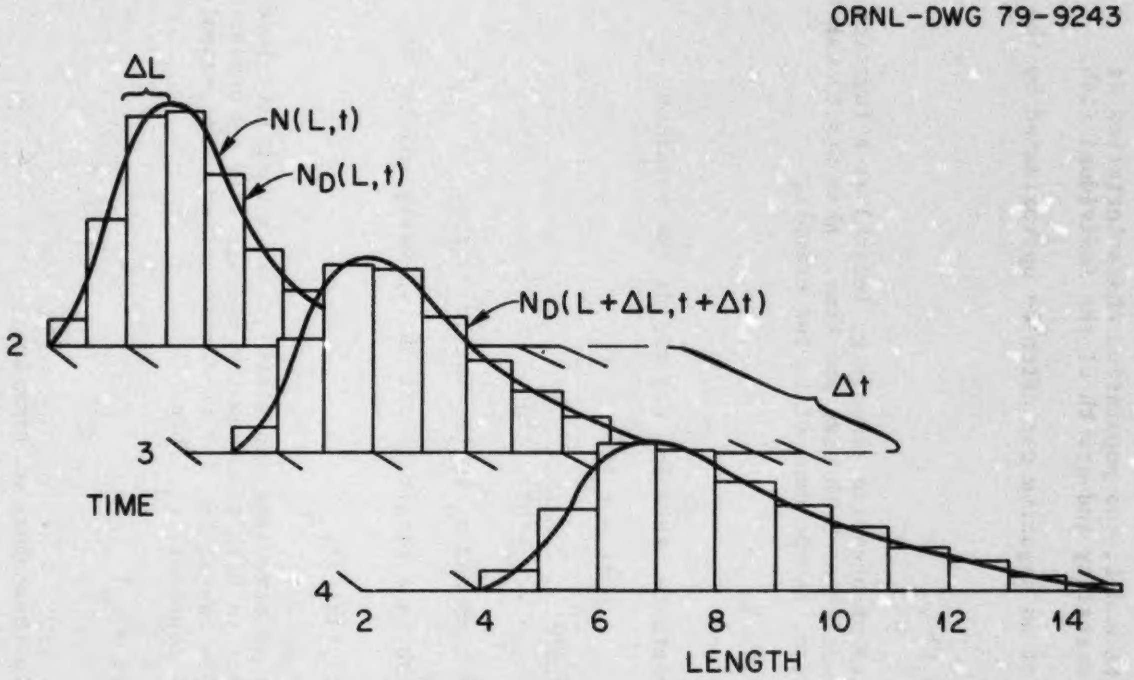


Figure 7. The three curves represent size distributions at three successive time intervals. The distributions $N(s,t)$ is a continuous distribution, while $N_D(L,t)$ is a discrete approximation of this distribution.

$$\begin{aligned} N(s,t + \Delta t) = N(s,t) & \\ & - \{\text{number of fish lost to mortality}\} \\ & - \{\text{number of fish lost because of growth to the next larger size class}\} \\ & + \{\text{number of fish entering because of growth from the next smaller size class}\} \\ & + \{\text{newly reproduced fish of size } s\} \\ & + \{\text{immigration from other populations}\} \\ & - \{\text{emigration to other populations}\}. \end{aligned} \tag{6}$$

Ignoring immigration and emigration, the conceptual model will be expressed in mathematical terms. The following assumptions and equations form the basis for this model.

Number of Fish Lost to Mortality--
Assume this is proportional to the number of fish in size class s, $N(s,t)$, the mortality coefficient, $Z(s,t)$, and the time interval, Δt.

Number of Fish Lost Because of Growth to the Next Larger Size Class--
Assume this is proportional to the number of fish in size class s, $N(s,t)$, and the fraction of that size which grows to the next larger size class, $G(s,t)\ (\Delta t/\Delta s)$. To help understand this term, note that $G(s,t)\ \Delta t$ represents the amount of a particular size class population that moves from one size class to the next during interval Δt, so $G(s,t)\ (\Delta t/\Delta s)$ is the fraction of a given size class population that moves.

Number of Fish Gained (Recruited) Because of Growth from Next Smaller Size Class--
Analogous to the above, this is $G(s - \Delta s,t)(\Delta t/\Delta s)N(s-\Delta s,t)$.

Number of Fish Gained in Size Class s from Reproduction--
This is a product of the number of reproductives, $N_{rep}(t)$, the fecundity, $M(t)$, and the fraction, $\Upsilon(s)$, of the fecundity going into size class s; i.e., $B(s,t) = N_{rep}(t)M(t)\Upsilon(s)$.

Combining the above terms yields

$$\begin{aligned} N(s,t + \Delta t) = N(s,t) - \Delta t Z(s,t)N(s,t) - (\Delta t/\Delta s)G(s,t)N(s,t) \\ + (\Delta t/\Delta s)G(s - \Delta s,t)N(s - \Delta s,t) + B(s,t)\Delta t \ , \end{aligned} \tag{7}$$

for the numbers of size s at time $t + \Delta t$ (Fig. 7). To obtain a governing equation from Eq. (7), rearrange (7) as

$$\begin{aligned} \frac{N(s,t + \Delta t) - N(s,t)}{\Delta t} + \frac{G(s,t)N(s,t)}{\Delta s} - \frac{G(s - \Delta s,t)N(s - \Delta s,t)}{\Delta s} \\ = -Z(s,t)N(s,t) + B(s,t) \end{aligned} \tag{8}$$

and take the limits

$$\lim_{\Delta t \to 0} \frac{N(s,t + \Delta t) - N(s,t)}{\Delta t} \equiv \frac{\partial N(s,t)}{\partial t} \quad (9)$$

$$\lim_{\Delta t \to 0} \frac{(G(s,t)N(s,t) - G(s - \Delta s,t)N(s - \Delta s,t)}{\Delta s} \equiv \frac{\partial}{\partial s}(G(s,t)N(s,t)). \quad (10)$$

to obtain

$$\frac{\partial N(s,t)}{\partial t} + \frac{\partial}{\partial s} \{G(s,t)N(s,t)\} = -Z(s,t)N(s,t) + B(s,t). \quad (11)$$

This equation must be supplemented with initial conditions on $N(s,t)$ at the initial time, t_0. In the remainder of this report, we shall let $t_0 = 0$ and assume that this instant precedes production of any of the cohort, so that

$$N(s,0) = 0 \text{ (for all s)} . \quad (12)$$

Equation (11) is the general cohort model used in this report. Appendix A shows how this equation can be solved analytically, at least to the point where only certain integrals are left to be done numerically. This appendix also presents certain limiting cases in which the solutions are completely analytic. The remaining appendices describe the computer programs that numerically solve the general model in which both the growth rate, $G(s,t)$, and the mortality rate, $Z(s,t)$, are size and time dependent and in which the reproduction (or recruitment) rate, $B(s,t)$, varies over a spawning period.

Appendix A also describes two further generalizations of the model. First, rather than being necessary to prescribe a reproductive rate, $B(s,t)$, it is possible simply to prescribe an initial size distribution, $N_0(s)$ at time t_0. Second, rather than each fish in the cohort being given the same growth rate, $G(s,t)$, there is a provision for dividing the cohort into subcohorts, each subcohort with its own growth rate, $G_i(s,t)$.

DATA SOURCE

A large volume of computer-based fisheries data is available for Barkley Reservoir and TVA's Cumberland Steam-Electric Plant. As a consequence, this system (plant and reservoir) was chosen as a test case for the model. The gizzard shad (Dorosoma cepedianum) was chosen as an example species because of its common occurrence in impingement samples and widespread distribution. Also, it is not as subject to winter kill as the threadfin shad (D. petenense) and this, coupled with greater longevity, results in more nearly stable populations.

The plant, reservoir, and attendant gizzard shad population are described in greater detail below.

BARKLEY RESERVOIR

Barkley Reservoir is a mainstream impoundment on the lower Cumberland River. Barkley Dam, located at Cumberland River Mile (CuRM) 30.6 near Grand Rivers, Kentucky, was closed in 1964. The reservoir extends approximately 103 km to Cheatham Dam (CuRM 148.7). At normal full pool (108 m above MSL) Barkley Reservoir has a surface area of 23,440 ha and a shoreline length of 1,615 km. Barkley Reservoir is connected with Kentucky Reservoir (a Tennessee River impoundment) by Barkley Canal, allowing integrated operation of the two reservoirs for navigation, flood control and hydroelectric power production.

CUMBERLAND STEAM-ELECTRIC PLANT

Physical Features

Cumberland Steam-Electric Plant is located on the south bank of Barkley Reservoir in Stewart County, Tennessee, at Cumberland River Mile (CuRM) 103 (Figure 8). This facility is the Tennessee Valley Authority's largest fossil fuel plant, having two units rated at 1,300 MWe each. The first unit began commercial operation in March 1973 and the second unit began operation in November 1973.

Condenser cooling water is provided for this plant thorugh a 200-m long intake channel located perpendicular to the shoreline (Figure 9). A 339-m long skimmer wall located at the mouth of the intake channel allows selective withdrawal of cooling water from the lower reaches of the reservoir. Maximum total condenser and auxiliary flow is 120 m^3/sec.

The intake pumping station at Cumberland Steam-Electric Plant consists of eight condenser cooling water pumps which draw water through sixteen intake chambers. At the mouth of each intake chamber are trash racks which keep out large debris. Behind the trash racks are the vertical traveling screens. These are a series of 2.3 m by 0.6 m interlocking screen panels attached to endless chains which rotate on sprockets located at the top and bottom of this intake structure. The screen panels consist of 12-gauge galvanized wire having 9.5 mm square openings.

Impingement

Impingement of fish on the screens at cooling water intakes constitute a potential adverse ecological impact. In response to the passage of Section 316(b) of the Clean Water Act, the Tennessee Valley Authority began a weekly fish impingement monitoring program at Cumberland Steam-Electric Plant in August 1974. Each Tuesday, all vertical traveling screens in operation were rotated and washed clean of fish and debris. Twenty-four hours later, the screens were again cleaned and the impinged fish flushed into a sluice pipe leading to a catch basin. All fish were separated by species into 25 mm length groups and total numbers and weights were recorded by species and 25-mm group.

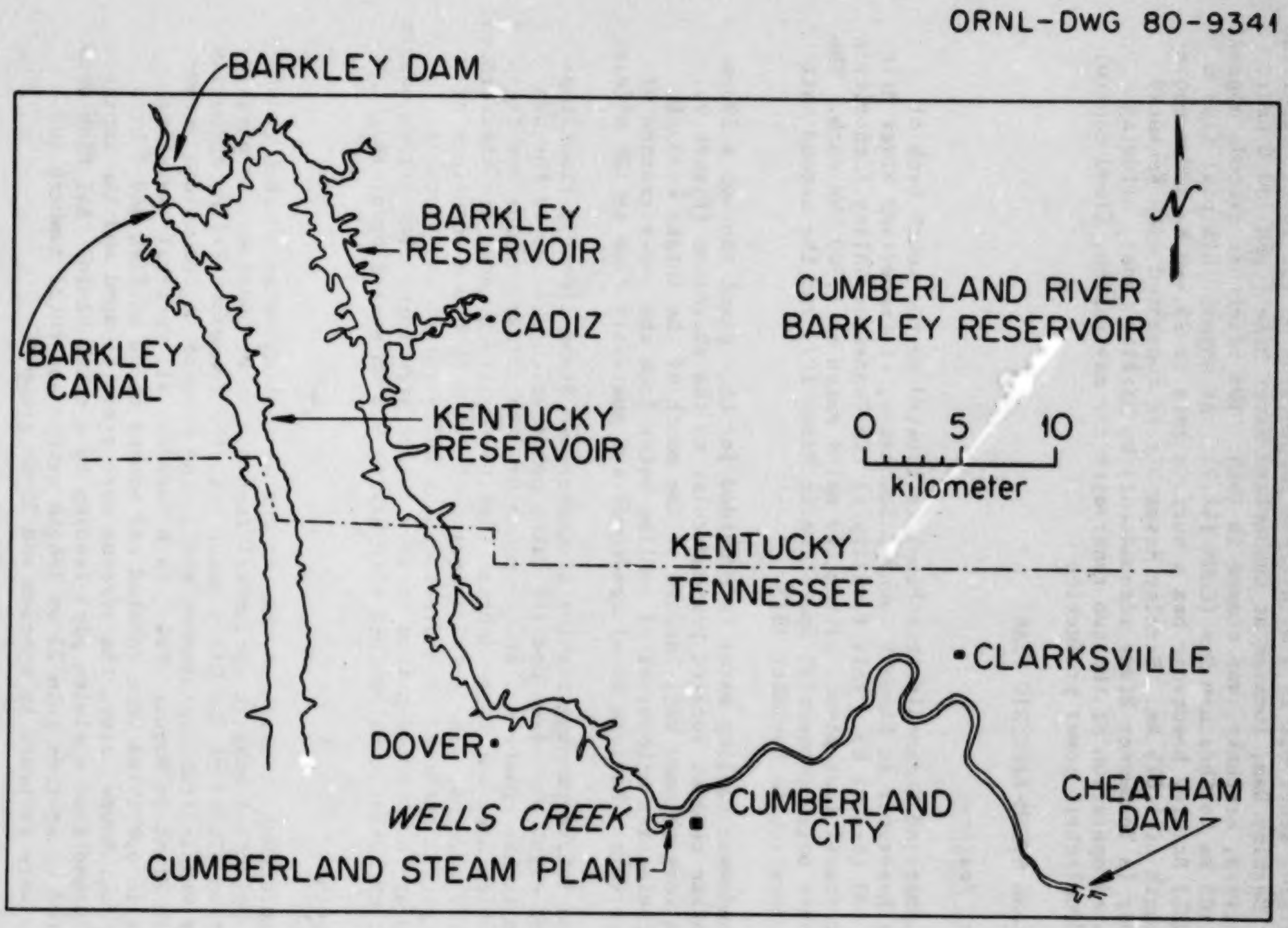
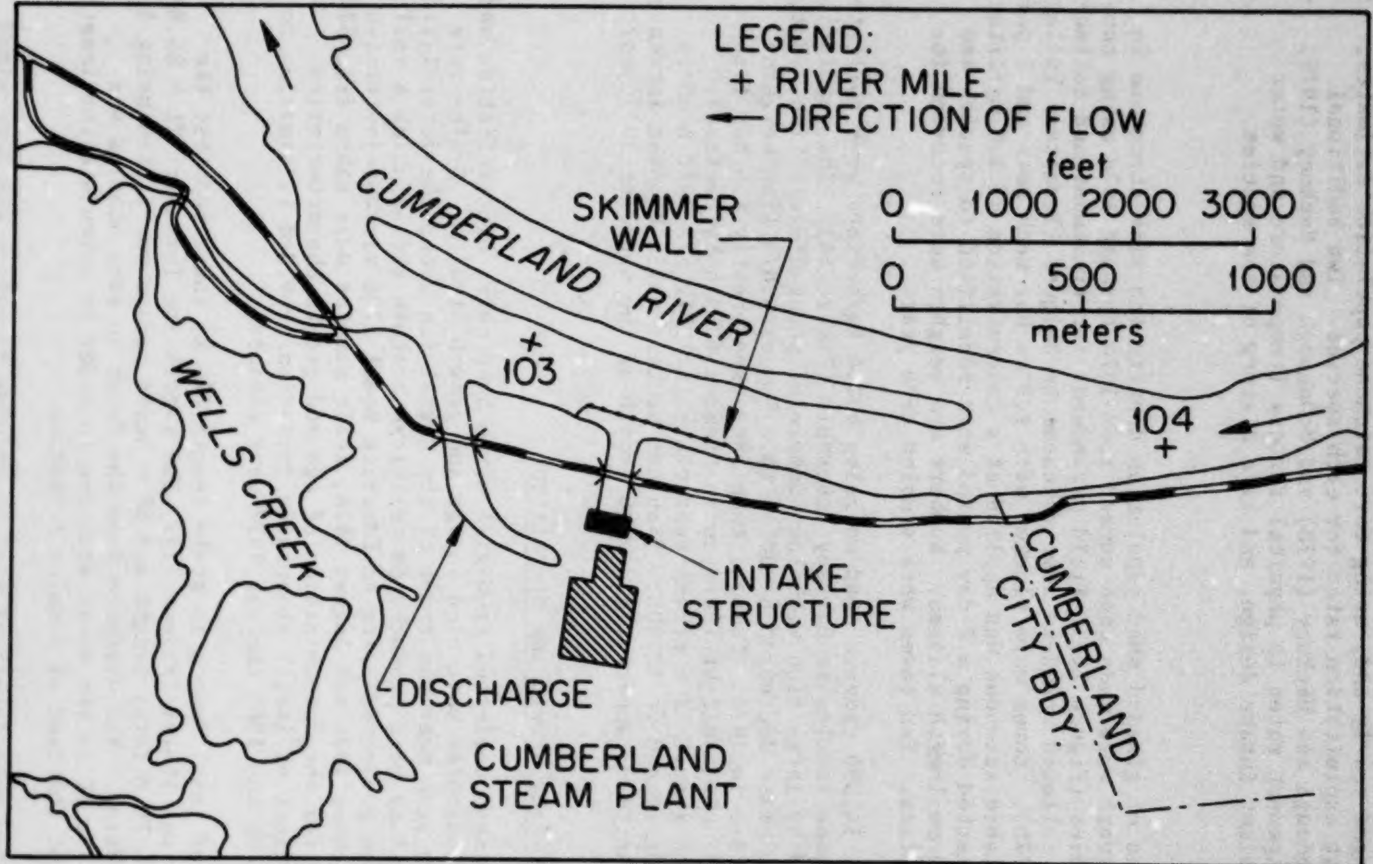

ORNL-DWG 80-9341
BARKLEY DAM
BARKLEY RESERVOIR
CADIZ
BARKLEY CANAL
KENTUCKY RESERVOIR
N
CUMBERLAND RIVER
BARKLEY RESERVOIR
0
5
10
kilometer
KENTUCKY
TENNESSEE
CLARKSVILLE
DOVER
WELLS CREEK
CUMBERLAND CITY
CUMBERLAND STEAM PLANT
CHEATHAM DAM

Figure 8. Location of Cumberland Steam-Electric Plant on Barkley Reservoir.

ORNL-DWG 80-9340


LEGEND:
+ RIVER MILE
← DIRECTION OF FLOW
feet
0 1000 2000 3000
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meters
CUMBERLAND RIVER
SKIMMER WALL
+ 103
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WELLS CREEK
INTAKE STRUCTURE
DISCHARGE
CUMBERLAND STEAM PLANT
CUMBERLAND CITY BDY.

Figure 9. Intake and associated structures at Cumberland Steam-Electric Plant.

Results of this monitoring program have been presented previously (Tennessee Valley Authority, 1977a). This study estimated the total numbers impinged yearly and, using cove rotenone population estimates, computed plant exploitation rates for each species. Two additional studies, McDonough and Hackney (1978) and McDonough and Hackney (1979) related impingement rates to physical factors (temperature and water elevation), plant intake design, and life history of the species.

GIZZARD SHAD

Estimates of gizzard shad population density and size structure in Barkley Reservoir were made each summer from 1974 through 1978 using cove rotenone samples (Figure 10). Field procedures for treatment and collection of data followed standard cove rotenone techniques (Tennessee Valley Authority 1977b). Coves were blocked with 1.3 cm bar mesh nets and 5 percent emulsifiable rotenone was applied at a concentration of 1.0 mg/liter. All fish collected during a 2-day period were identified to species and grouped by 25 mm length classes. Numbers and weights were recorded for each length class. Ten coves were sampled each year.

In 1974, 14,390 gizzard shad weighing 692.4 kg/hectare were collected in cove rotenone samples in Barkley Reservoir (Figure 14). The population was dominated by large fish with low numbers of young-of-year fish. Both numbers and biomass decreased steadily to a low of 4,873 fish weighing 191.7 kg/hectare in 1976. Numbers then increased greatly (15,369 fish/hectare) with only a slight increase in biomass (229.6 kg/hectare), apparently the result of a strong year class in 1977. In 1978 numbers per hectare decreased to 12,906.4 fish per hectare while biomass increased to 365.7 kg/hectare, apparently due to growth of the abundant 1977 year class.

Estimation of Age, Growth and Mortality

Gizzard shad collected from gill nets, hoop nets, electrofishing and cove rotenone samples were used in age and growth studies. Scales were taken from an area near the front of the dorsal fin above the lateral line. Scale impressions were produced on cellulose acetate strips using a roller press and then projected using an Ederback model 2700 microprojector (40 X). Between September 1974 and August 1978, scale samples were taken from 679 gizzard shad for the determination of age and growth characteristics. Back calculations of length at annulus formation provided information on growth rates of the 1969 through 1977 year classes.

A plot of total length to scale length (40 X) indicated that the relationship was linear (Figure 11). The regression formula: $TL = 85.86 + 0.83\ SR$ where TL = total length and SR = scale radius was fitted using least square procedures. The distance from the focus to each annulus was substituted for SR in the above equation in order to calculate the length of the fish at the time of annulus formation.

Calculated mean length of fish at annulus formation was determined for each age group collected for the 1969 through 1977 year classes (Table 1). Growth was most rapid during the first year and then decreased. Weighted

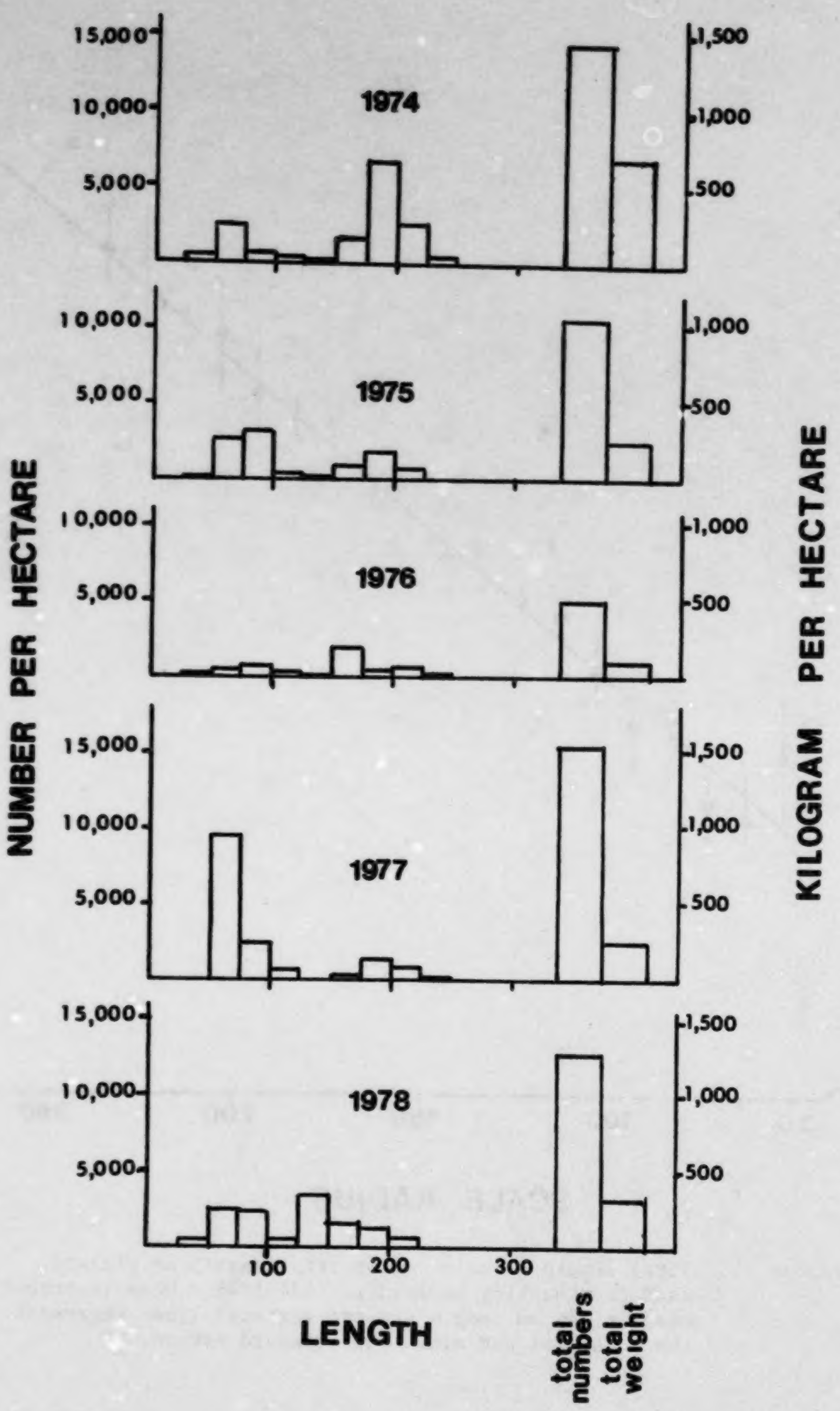

Figure 10. Total biomass (kilograms per hectare) distribution of gizzard shad in Barkley Reservoir, 1974-1978.

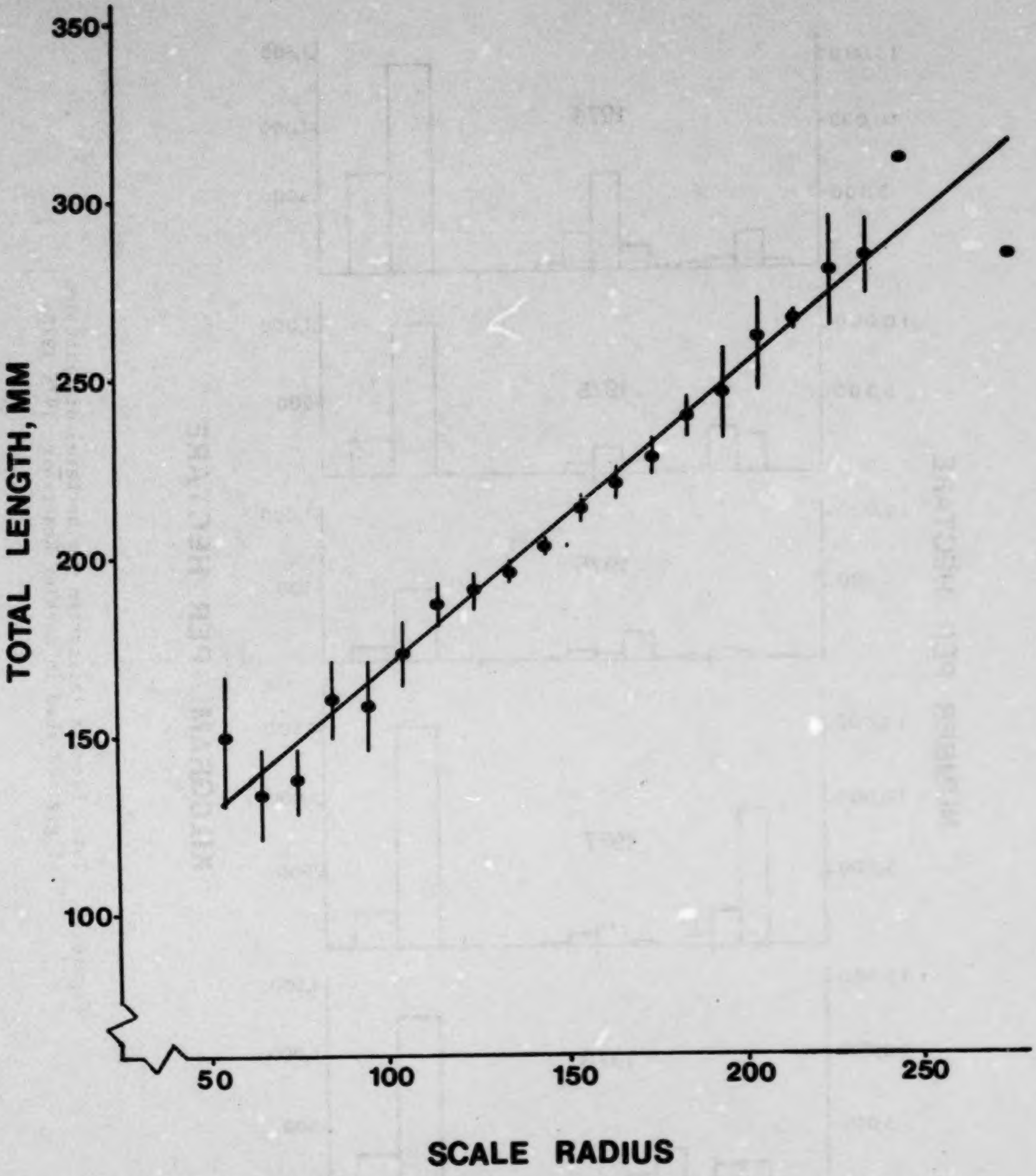

Figure 11. Total length - scale radius relationship of gizzard shad from Barkley Reservoir, 1974-1978. Dots represent means of 10 mm length groups; vertical lines represent the mean plus and minus two standard errors.

mean increments for years I-IV were 144.2, 41.1, 15.7, 12.5, and 28.5. The increment for age V is of doubtful accuracy, because this estimate is based upon a single fish. Lee's phenomenon of apparent change in growth rates was evident.

TABLE 1. MEAN ESTIMATED TOTAL LENGTH (mm) AT EACH ANNULUS FOR GIZZARD SHAD COLLECTED IN BARKLEY RESERVOIR (1974-1978)

Age Group	Number of Fish	Annulus I	II	III	IV	V
I	237	149.47				
II	266	143.55	190.13			
III	122	136.97	177.44	202.20		
IV	19	133.79	169.29	192.93	212.54	
V	1	144.08	191.48	206.46	232.24	243.05
Numbers		645	408	142	20	1
Grand mean						
Length		144.19	185.32	200.99	213.53	242.05
Increments		144.19	41.13	15.67	12.54	28.52

Growth rates tended to increase from 1969 through 1976 (Figure 12), perhaps in response to decreasing stock density. Barkley Reservoir was impounded in 1964. Since fish population density has been shown to decrease following impoundment, the increasing growth rates may be a result of decreasing stock density.

Scales were taken from representative individuals in each 25 mm length group (> 100 mm) collected in 1977 and 1978 cove rotenone samples for determination of fish age. Using the proportion of individuals of each age in the subsample, age composition for each 25 mm size group was determined (Tables 2 and 3). Fish smaller than 100 mm were assumed to be young-of-year. Figure 13 shows length frequencies by age groups and for the entire population.

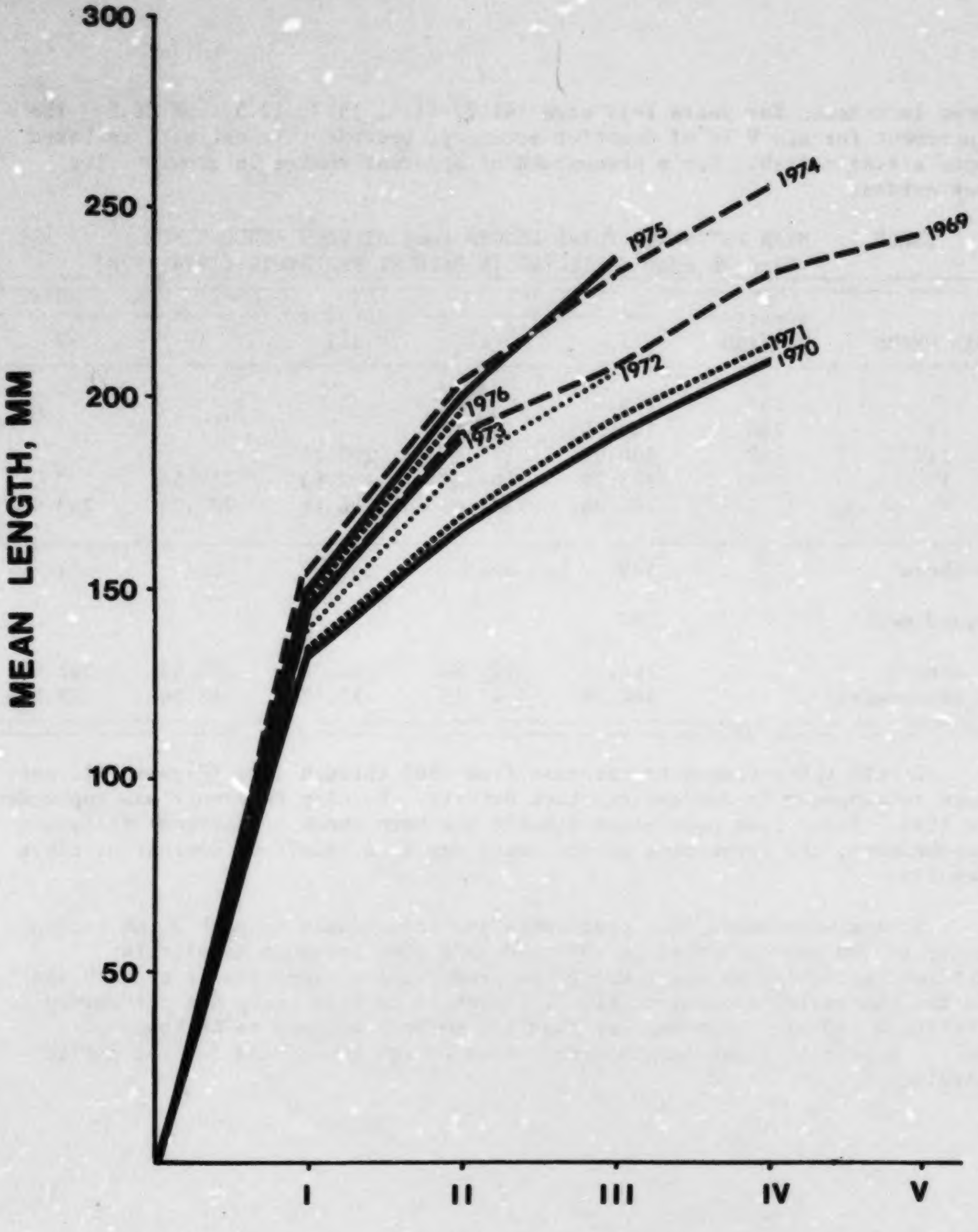

Figure 12. Comparison of back calculated growth rates of gizzard shad for the 1969 through 1976 year classes.

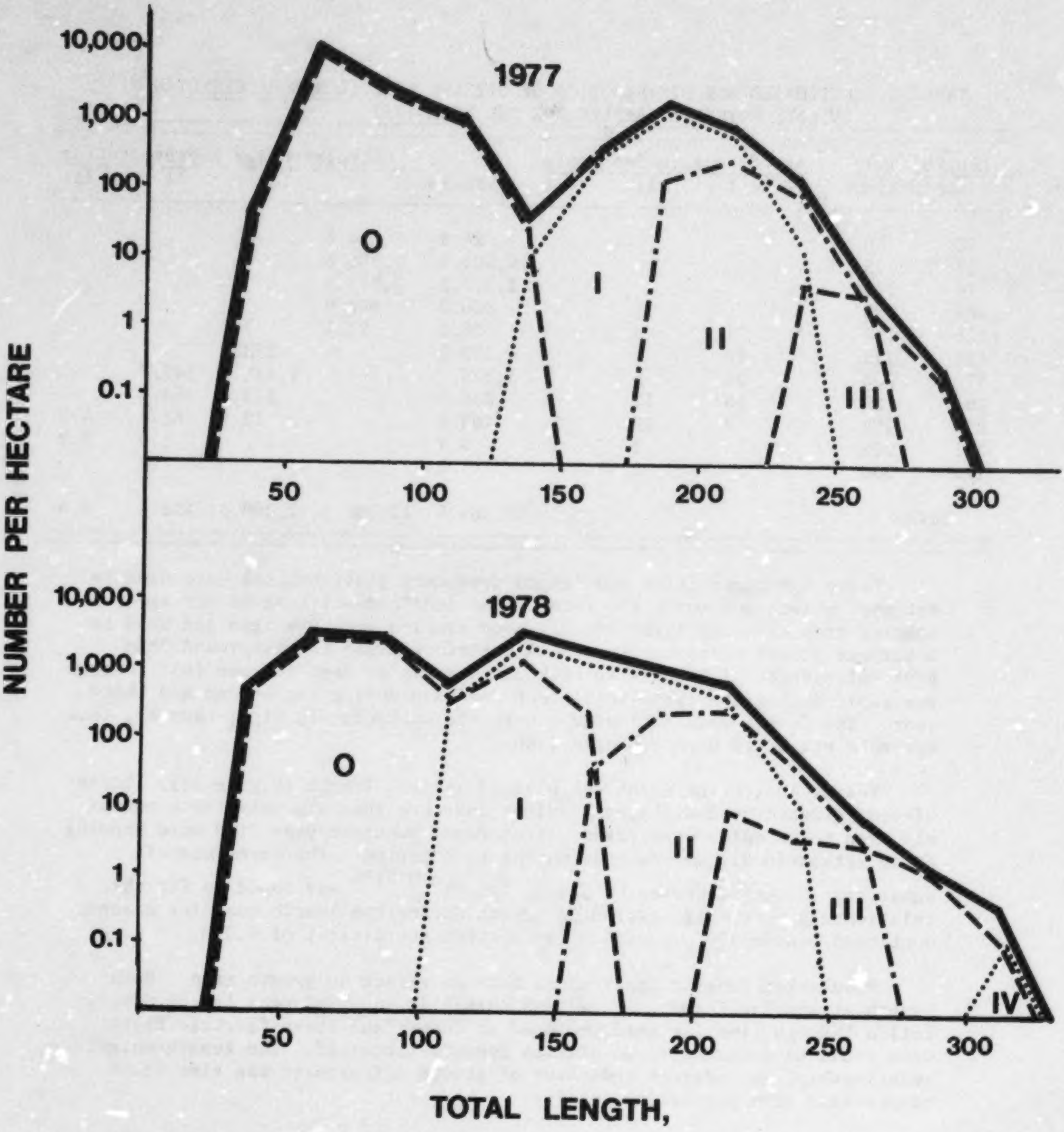

Figure 13. Estimated length frequency distribution of gizzard shad in 1977 and 1978 cove rotenone samples.

TABLE 2. ESTIMATED AGE DISTRIBUTION OF GIZZARD SHAD (DOROSOMA CEPEDIANUM) IN COVE ROTENONE SAMPLES FOR THE YEAR 1977

Length (mm)		Age Groups in Subsample					Calculated Age Representation			
Minimum	Maximum	0	I	II	III	Fish/ha	0	I	II	III
26	50					24.8	24.8			
51	75					9,506.6	9,506.6			
76	100					2,377.5	2,377.5			
101	125	9				866.0	866.0			
126	150	3	1			28.1	21.1	7.0		
151	175		18			293.3		293.3		
176	200		24	3		1,329.1		1,181.4	147.7	
201	225		24	11		836.9		573.9	263.0	
226	250		3	20	1	103.0		12.9	85.8	4.3
251	275			2	3	3.9			1.6	2.3
276	300			1		.2			.2	
TOTAL						15,369.4	12,796	2,068.5	498.3	6.6

These age composition and length frequency distributions were used to estimate growth and mortality rates. The length distributions and age subsamples from 1977 and 1978 cove rotenone samples were averaged and used to determine growth characteristics. A pattern similar to that found from back calculation of lengths at each annulus was evident (Figure 14). Growth was rapid during the first year, then declined during the second and third year. The fourth year estimated growth was unexpectedly high; however, this estimate was based upon a single fish.

Yearly length increment was plotted against length (Figure 15). Young-of-year gizzard shad averaged 77.91 mm and were approximately three months old when the samples were taken. Therefore, young-of-year fish were growing at an estimated 312 mm per year during this period. The experimental equation: $\text{Length Increment} = 504.32\ \text{length}^{-0.0134}$ was found to fit this relationship very well (excluding growth during the fourth year for reasons mentioned previously), having a correlation coefficient of 0.990.

Population density appeared to have an effect on growth rate. Both length at annulus formation, and the change in young-of-year length distribution through time for shad impinged at Cumberland Steam-Electric Plant were found to decrease as population density increased. The length-weight relationship, an indirect indicator of growth differences was also found to decrease with population density.

Back calculated length at first annulus formation and length increment between the first and second annulus both tended to decrease with increasing population density (Figure 16). The 1974 year class showed a high growth rate despite high population density. The estimated growth rate for 1974, however, was based upon only five individuals while estimates of growth of the 1979, 1976, and 1977 year classes were based on 49, 144, and 156 individuals, respectively.

TABLE 3. AGE DISTRIBUTION OF GIZZARD SHAD (DOROSOMA CEPEDIANUM) IN COVE ROTENONE SAMPLES FOR THE YEAR 1978 AS DETERMINED BY SCALE READINGS OF SUBSAMPLES FROM EACH SIZE GROUP.

Length (mm)		Age Group in Subsample						Calculated Age Representative				
Maximum	Minimum	0	I	II	III	IV	Fish/ha	0	I	II	III	IV
26	50						474.3	474.3				
51	75						2,527.5	2,527.5				
76	100						2,353.5	2,353.5				
101	125	1	1				684.2	342.1	342.1			
126	150	13	22				3,386.1	1,257.7	2,128.4			
151	175	7	39	1			1,648.9	245.6	1,368.2	35.1		
176	200		42	12			1,055.2		820.7	234.5		
201	225		50	32	1		711.7		428.7	274.4	8.5	
226	250		8	27	3		56.8		12.0	40.4	4.5	
251	275			4	6		6.7			2.7	4.0	
276	300				3		1.2				1.2	
301	325				1	1	0.3				.1	.1
TOTAL							12,906.4	7,200.7	5,100.1	587.1	18.3	.1

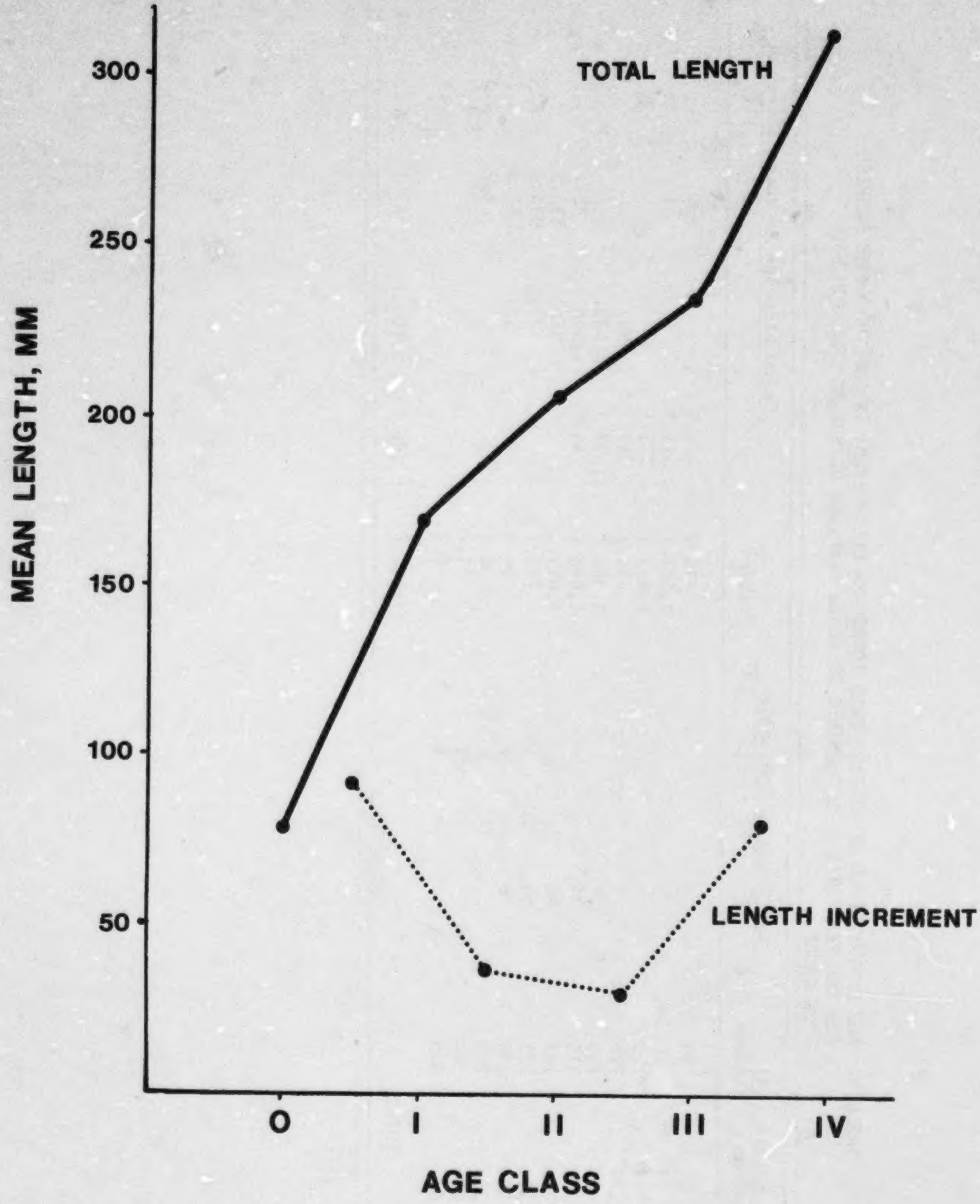

Figure 14. Mean length and mean length increment of gizzard shad in 1977 and 1978 cove rotenone samples.

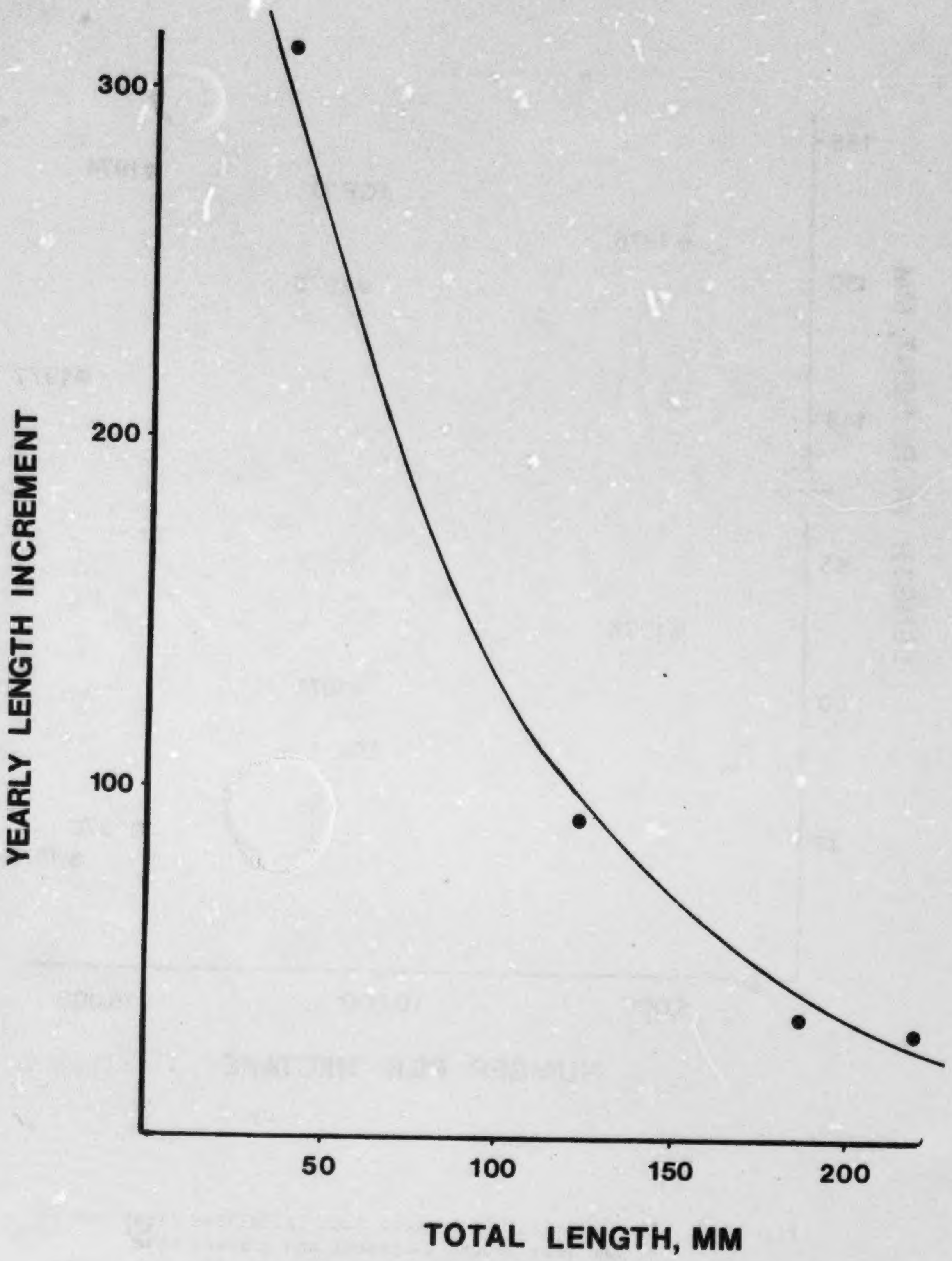

Figure 15. Yearly length increment versus total length.

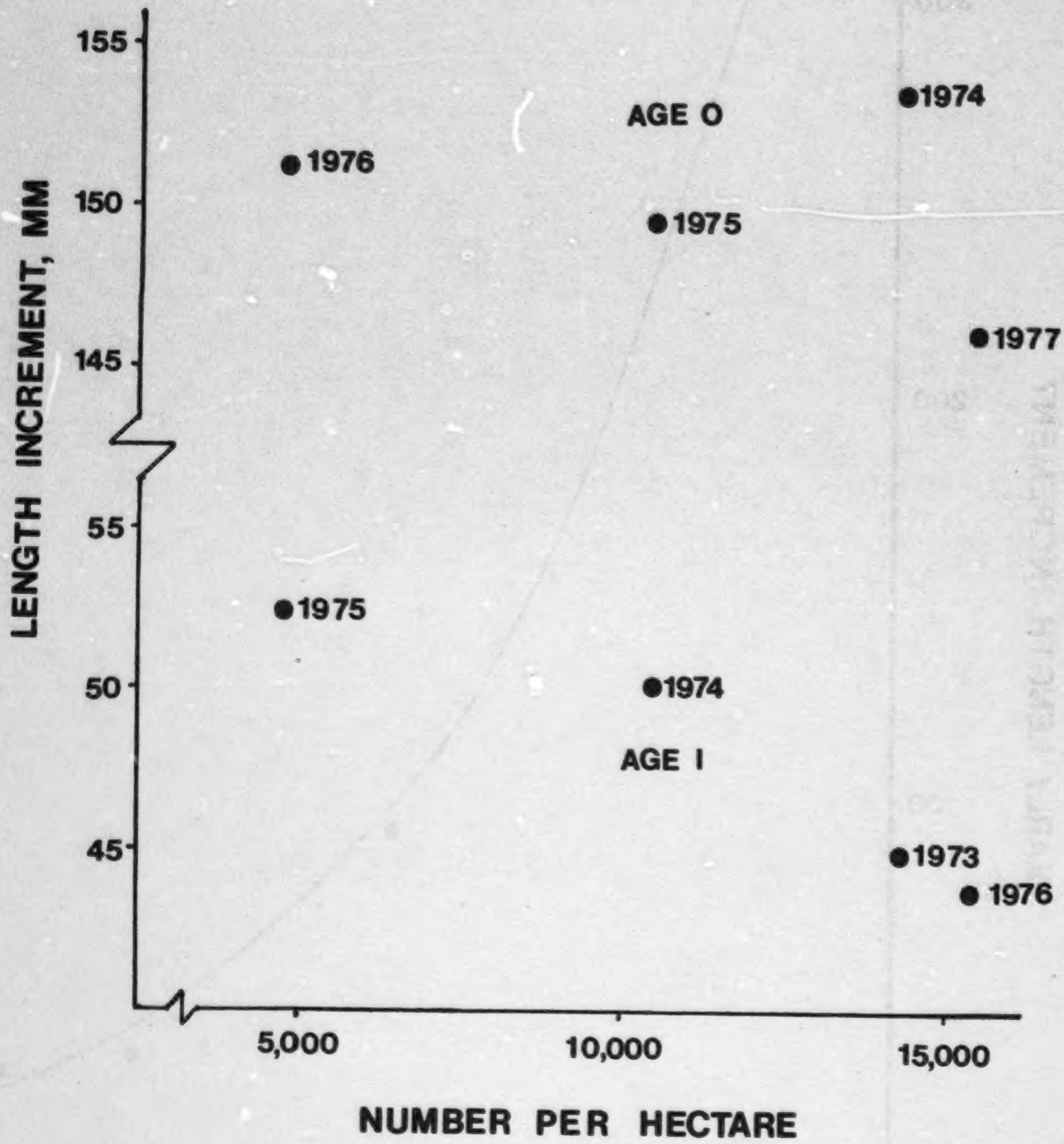

Figure 16. The relationship between back calculated first and second year length increment and gizzard shad population density.

The effect of population density on young-of-year gizzard shad growth rate was also reflected in the length-frequency distributions of fish impinged at Cumberland Steam-Electric Plant. Figure 17 is a 3-dimensional graph of the length distributions of gizzard shad impinged from May 1975 through April 1976. Numbers are expressed as logarithms to permit greater detail for all sizes. Young-of-year fish first became large enough to be impinged in late July or early August. Growth after this period resulted in a gradual increase in length distributions through the remainder of the year. Although this same pattern was observed each year, the rate of growth differed each year, apparently due to differences in stock density. The average length of young-of-year fish was computed for each month for the 1974, 1975, and 1976 year classes using length frequency analyses to separate young-of-year fish from older individuals. The growth rate increased each year (Figure 18), while population densities decreased.

In addition to its usefulness in converting length to weight, the length-weight relationship is also useful as an indicator of population growth differences. The relationship was computed for gizzard shad collected during the first day of cove rotenone samples. Fish were grouped into 25-mm groups, and numbers and weight of individuals in each size group were recorded. Mean weight per individual in each size group was computed by dividing the total weight by the number in the size class. The relationship: Log (weight) = -4.65 + 2.828 x log (length) describes this relationship having an R^2 of 0.97. The deviations from this regression for each year were plotted against population density (Figure 19). In years when numbers were low, the weight of fish at a given size tended to be higher than in years when densities were high. Sequential F-test (Draper and Smith, 1966) of the relationship between mean weight and population density (with length already in the model) indicates that this relationship is highly significant (Table 4).

TABLE 4. ANALYSIS OF VARIANCE FOR EFFECTS OF THE LOGARITHM OF LENGTH AND POPULATION DENSITY ON THE LOGARITHM OF WEIGHT

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F	Prob F
Corrected Total	471	471.0480			
Regression	2	216.1010	108.0504	7,294.60	0.0001
due to $\log_{10}$(length)	1	215.9516	215.9516	14,579.11	0.0001
due to density given $\log_{10}$ (length)	1	0.1494	0.1494	10.08	0.0016
Residual	469	6.9470	0.0148		

The average of the age distributions in the 1977 and 1978 cove rotenone samples was used to estimate annual total mortality rates. Numbers of gizzard shad (on log scale) for each age is plotted against age. The slope of the descending right limb describes the instantaneous mortality rate (Figure 20). Mortality rates were found to increase each year. Total

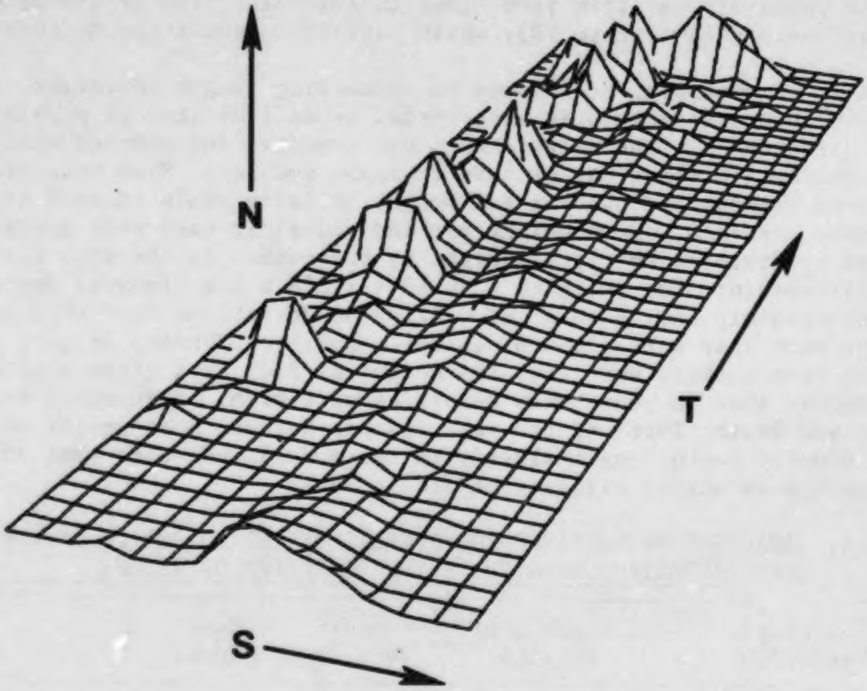

Figure 17. Three-dimensional graph of the logarithm of gizzard shad numbers impinged through time (May 1975 to April 1976) by 25 mm groups (N = numbers, T = time in weeks, S = size).

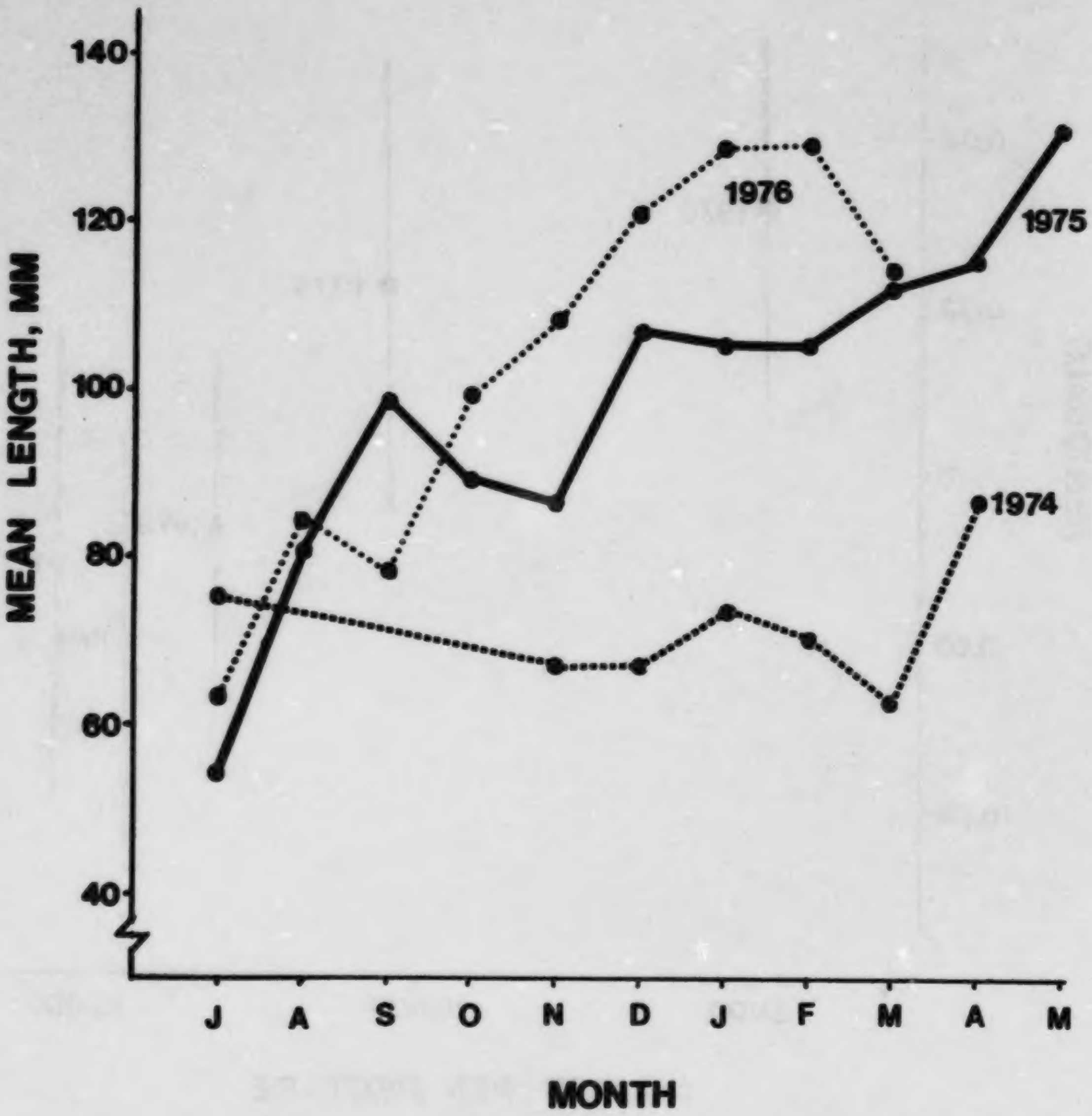

Figure 18. Mean length of the 1974, 1975 and 1976 year classes of gizzard shad impinged on the intake screens at Cumberland Steam Electric Plant by month.

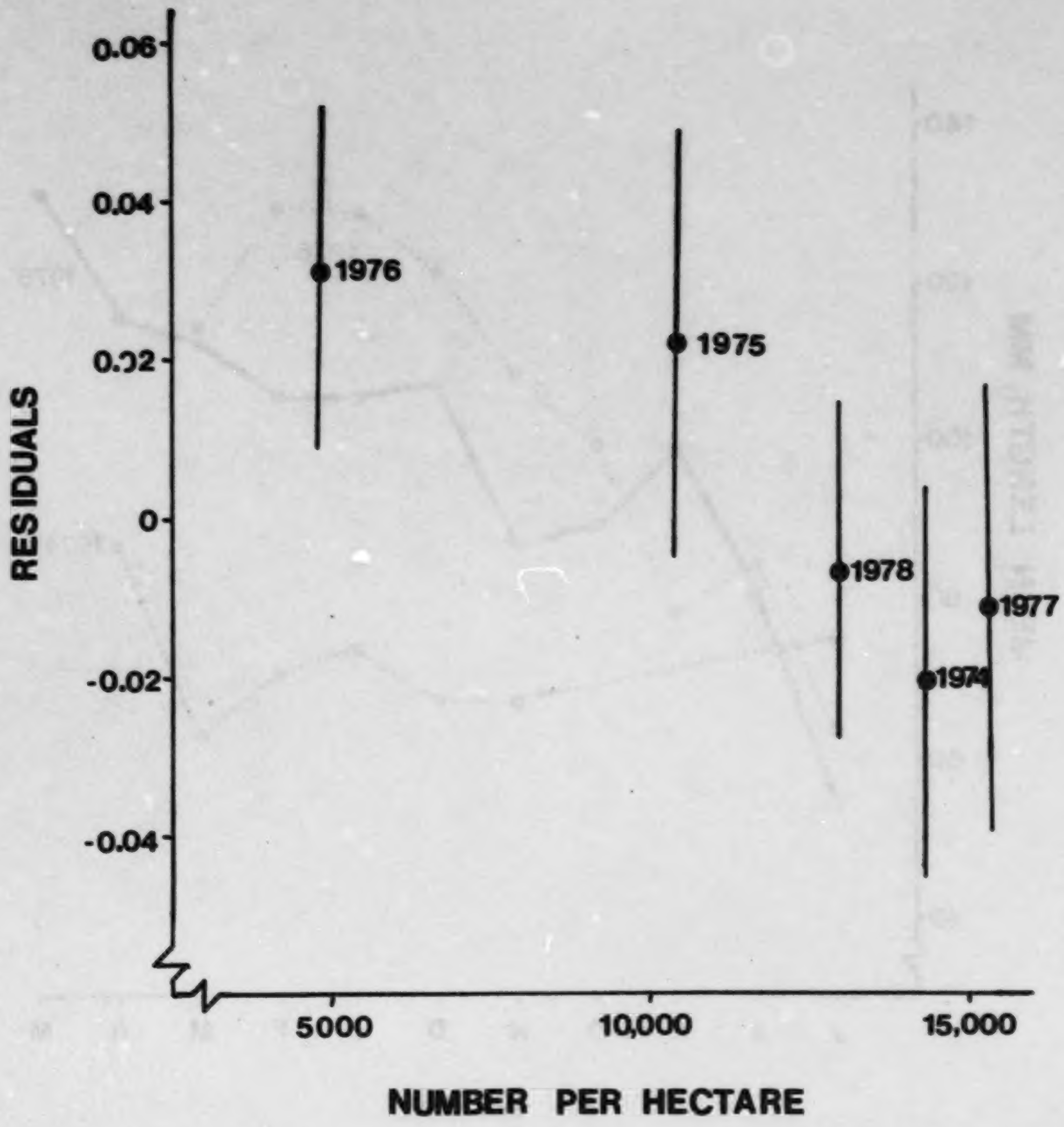

Figure 19. Residuals of the log length - log weight relationship as a function of population density.

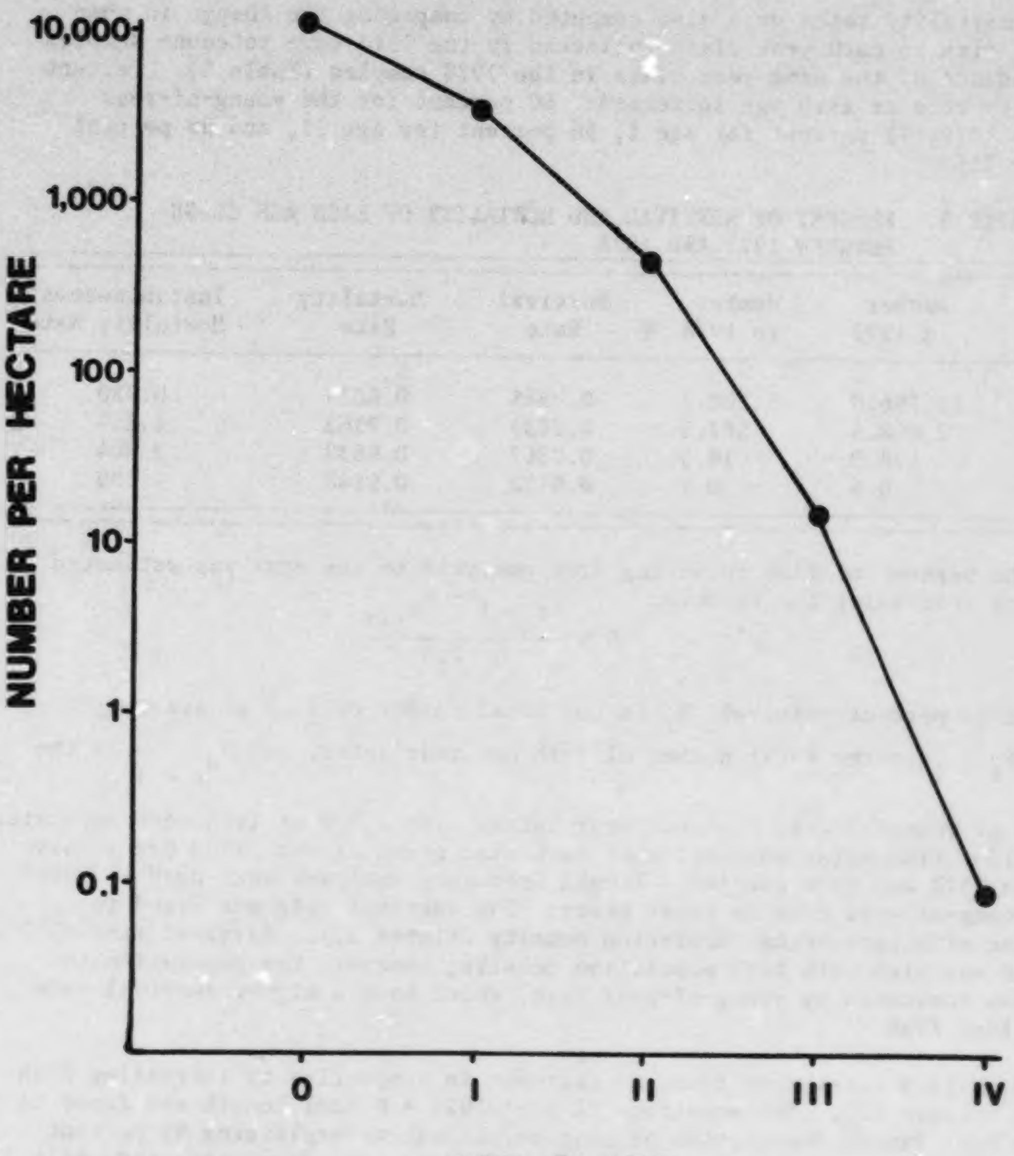

Figure 20. Density (number per hectare) of gizzard shad in Barkley Reservoir cove rotenone samples (average of 1977 and 1978 samples) by age class.

annual mortality rates were also computed by comparing the change in numbers of fish in each year class collected in the 1977 cove rotenone samples to abundance of the same year class in the 1978 samples (Table 5). Percent mortality rose as fish age increased: 60 percent for the young-of-year fish in 1977, 72 percent for age I, 96 percent for age II, and 98 percent for age III.

TABLE 5. PERCENT OF SURVIVAL AND MORTALITY OF EACH AGE CLASS BETWEEN 1977 AND 1978

Year Class	Number in 1977	Number in 1978	Survival Rate	Mortality Rate	Instantaneous Mortality Rate
1977	12,796.0	5,100.1	0.3985	0.6015	0.920
1976	2,068.5	587.1	0.2839	0.7162	1.259
1975	498.3	18.3	0.0367	0.9633	3.304
1974	6.6	0.1	0.0152	0.9848	4.189

The percent of fish surviving from one year to the next was estimated for each year using the formula:

$$S = \frac{N_{t+1} - N_{0_{t+1}}}{N_t}$$

where S is percent survival, N_t is the total number of fish at some time, N_{t+1} is the total number of fish one year later, and $N_{0_{t+1}}$ is the number of young-of-year fish one year later. The age 0 of fish were separated from older fish using subsamples of each size group as described previously for the 1977 and 1978 samples. Length frequency analyses were used to identify young-of-year fish in other years. The survival rate was found to decrease with increasing population density (Figure 21). Survival from 1977 to 1978 was high with high population density; however, the population in 1977 was dominated by young-of-year fish, which have a higher survival rate than older fish.

Mortality rates were found to increase in proportion to increasing fish length (Figure 22). The equation: $Z = -1.7926 + 0.0207$ length was found to be the best linear description of this relationship, explaining 81 percent of the variation. Second-year mortality, however, was over estimated while third-year mortality was under estimated. The increase in mortality rate with length (or age) is unexpected, mortality would be expected to be highest during the first year, due to heavy predation. As shad become larger, the mortality rate would be expected to decrease because they are no longer available as prey to most predatory fish (Bodola 1965).

An apparent increase in mortality with increasing age would result from migration of older individuals to open water areas. Bodola (1964) found that in western Lake Erie young-of-year and age I fish were close to shore in mid-summer; usually in shallow water quite close to shore. As gizzard shad became older, they were found to inhabit deeper water.

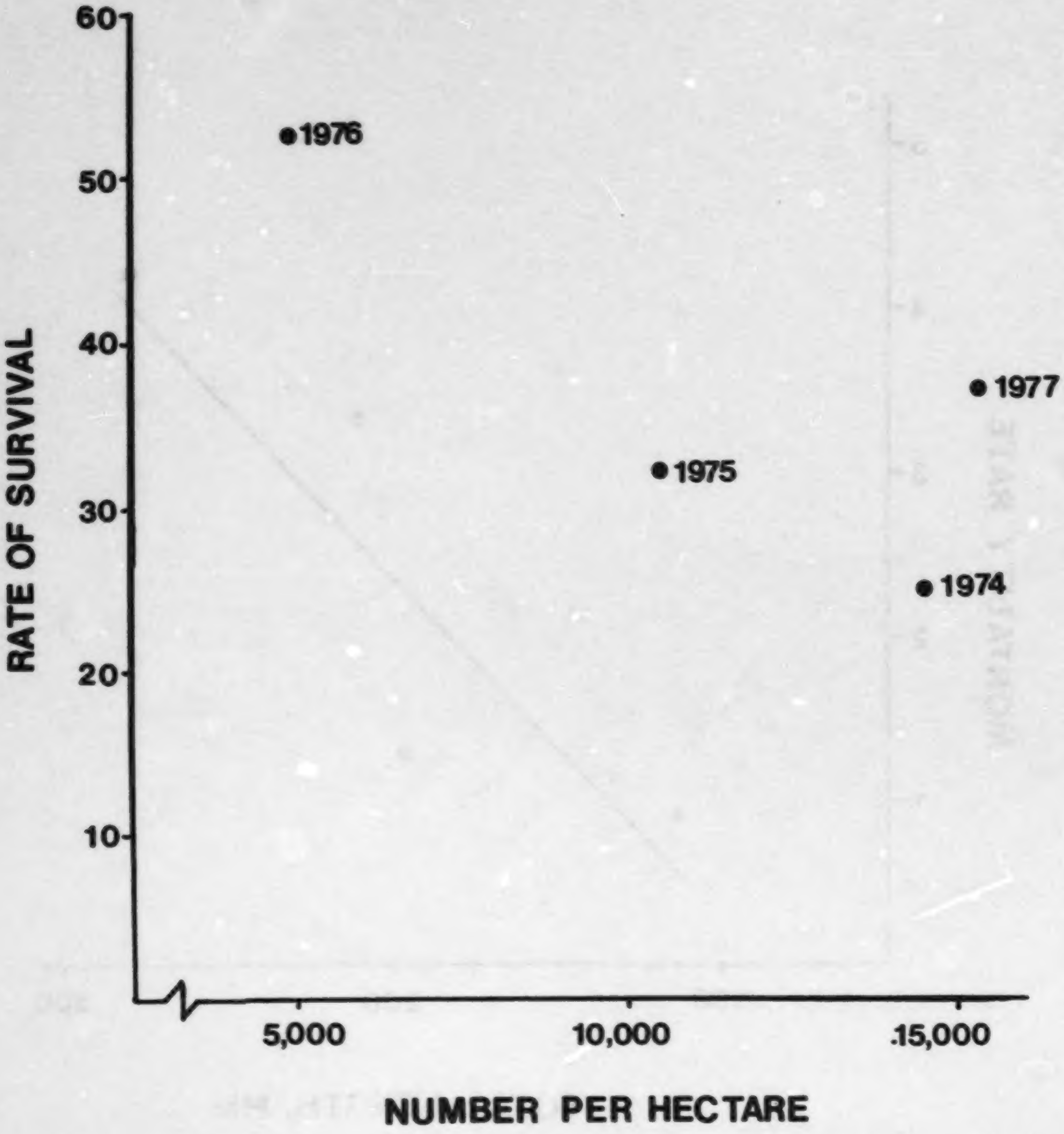

Figure 21. Relationship between survival rate of gizzard shad and population density.

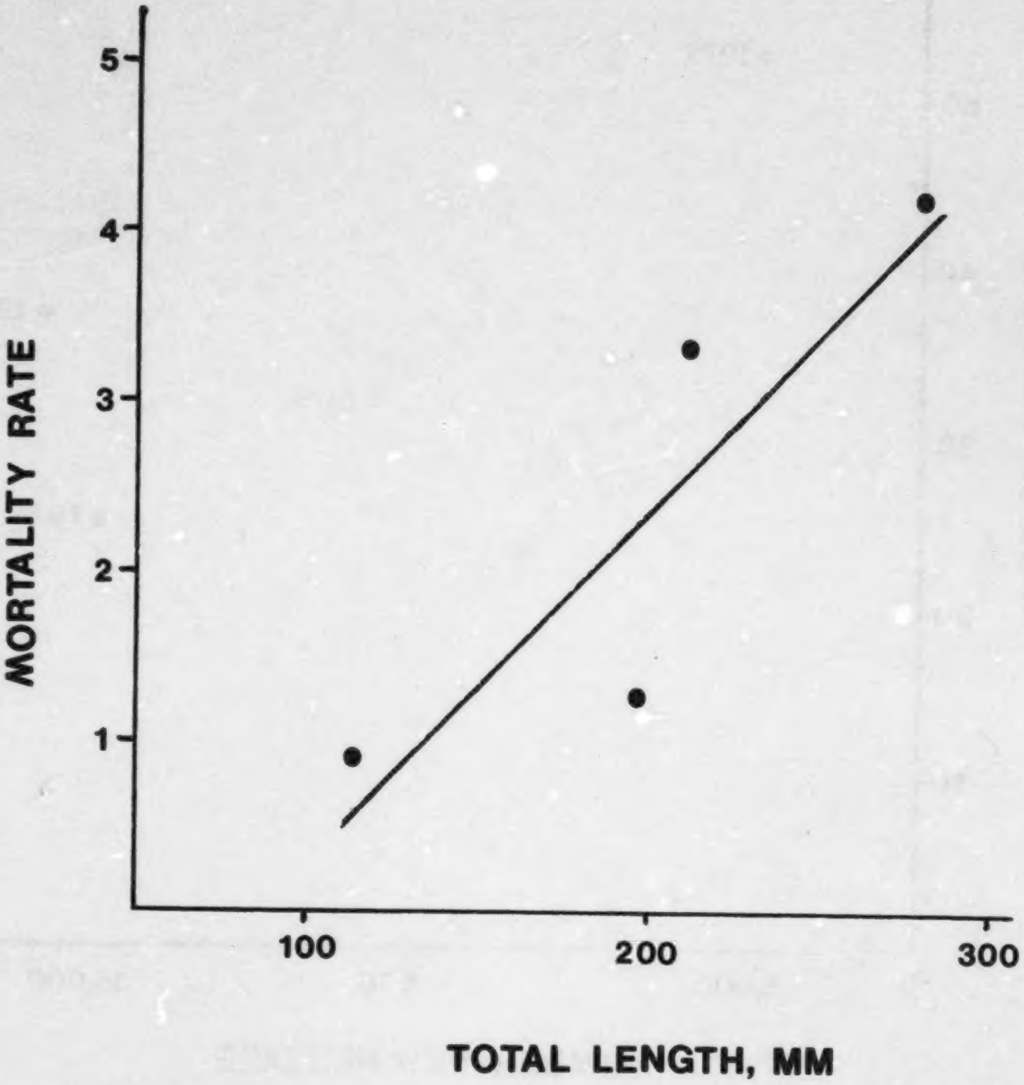

Figure 22. Increase in mortality rate with increasing length.

In order to examine the question of how well cove samples represent open water areas of a reservoir, the Reservoir committee of the Southern Division of the American Fisheries Society sampled Crooked Creek Bay (85 hectares) in Barkley Reservoir. This embayment was divided into cove and open water areas and treated with rotenone. The mouth of the bay was blocked with nets and the open water was divided by nets into three areas. All coves in the embayment were also blocked and the larger coves were subdivided into compartments.

Length distributions of gizzard shad collected from the small coves and ends of the large coves were compared with the open water areas (Figure 23). No evidence of migration of older fish from coves to open water was found. Most length groups between 63.5 mm and 317.5 mm were overestimated by the cove samples except for the 91.4 mm to 114.3 mm and the 218.4 mm to 241.3 mm groups. The open water samples tended to have more individuals smaller than 63.5 mm and larger than 317.5 mm, probably because the large sample area increased the likelihood of encountering individuals of these sizes.

The convex shape of the catch curve may be due to high population density. Michaelson (1970) and Anderson (1973) examined the dynamics of balanced and unbalanced bluegill (Lepomis macrochirus) populations in ponds. Balanced populations were defined as those with a satisfacotry relationship between the fish population and its food supply (Anderson 1973). Balanced populations were characterized by high and relatively stable recruitment of young-of-year, while unbalanced populations were characterized by wide variations in year class strength. They also found high mortality of young fish in balanced populations. Unbalanced populations had low natural mortality in young fish but high mortality for age II and older. Anderson (1973) discussed the similarities between characteristics of pond bluegill populations and gizzard shad populations where wide fluctuations in year-class strength may also be indicative of imbalance for reservoir populations of this species.

Estimates of annual impingement were determined by integrating the area between successive pairs of sample dates over a period from August 1 to July 31 for each year. The beginning of this period approximates both the first occurrence of a year class of gizzard shad on the intake screens and the cove rotenone sample period.

Between August 1974 and July 1975, an estimated 165,050 (7.04 per hectare) shad were impinged (Table 6). Impingement estimates decreased to 95,103 (4.06 per hectare) between August 1975 to July 1976. From August 1, 1976, to March 23, 1977, an estimated 190,267 fish were impinged. Expanding this figure to a full year yielded an estimated 296,828 (12.66 per hectare) gizzard shad impinged. This is probably an overestimate since fall and winter are usually the periods of highest impingement.

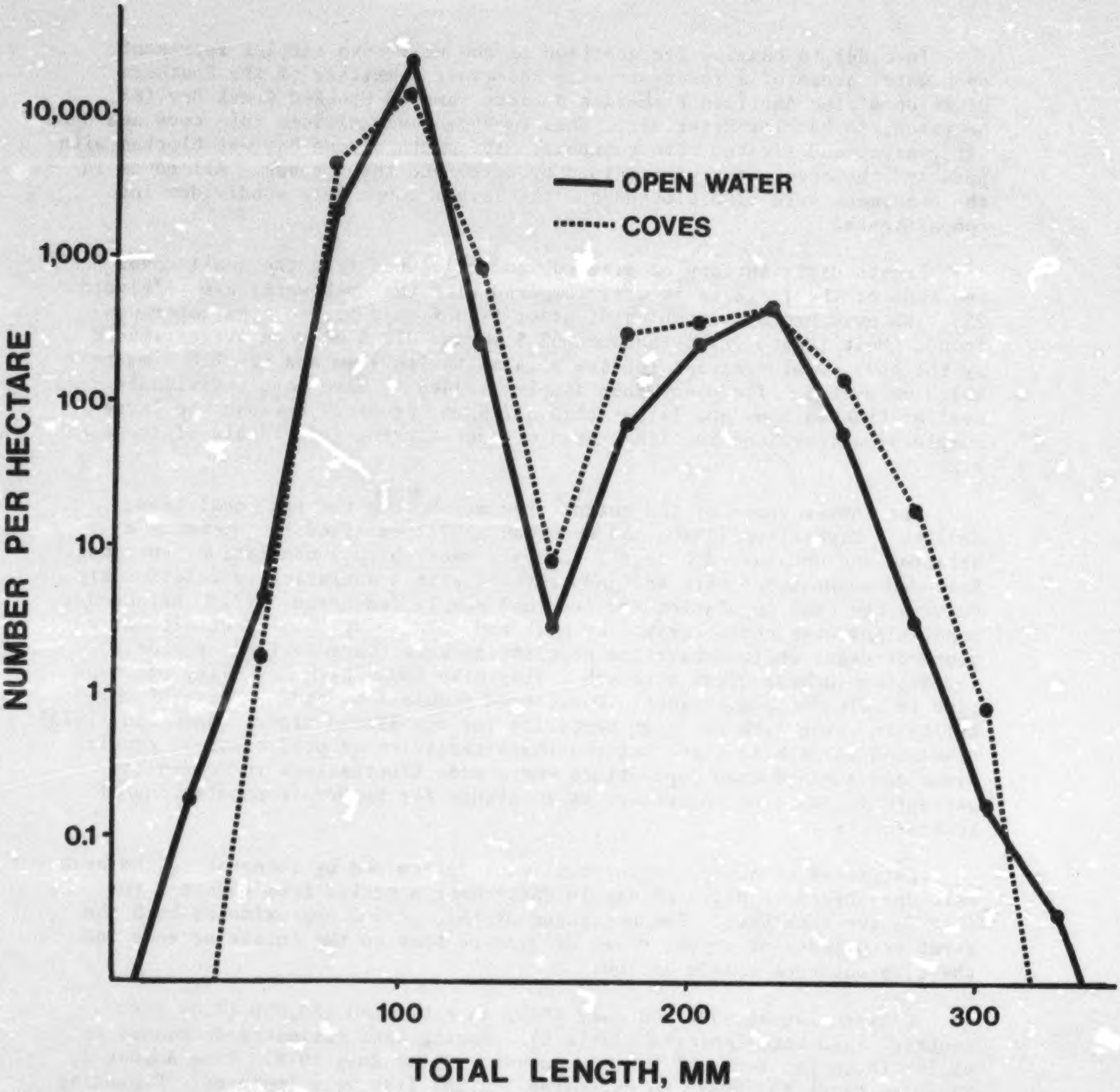

Figure 23. Length frequency distribution in cove samples compared with open water areas in the Crooked Creek embayment of Barkley Reservoir.

TABLE 6. COVE ROTENONE POPULATION DENSITY ESTIMATES, YEARLY IMPINGEMENT RATES,* ESTIMATES OF TOTAL, IMPINGEMENT AND NATURAL MORTALITY RATES, 1974-1977

	Numbers Per Hectare			Yearly Mortality Rate		
Year	Total Initial Population	Age I+ at End of Year	Numbers Impinged Per Year	Total	Plant	Natural
1974	14,390.09	3,582.92	7.04	1.3904	0.0020	1.3884
1975	10,484.93	3,380.84	4.06	1.1318	0.0012	1.1306
1976	4,872.59	2,573.40	12.66	0.6384	0.0049	0.6335
MEAN	9,915.87	3,179.05	7.92	1.1375	0.0025	1.1351

* From August to July.

Using abundance estimates obtained from cove rotenone samples, it was estimated that in the 1974-1975 season, 0.049 percent of the gizzard shad in Barkley Reservoir were impinged. This figure decreased to 0.039 percent in 1975-1976, and increased to 0.206 percent in 1976-1977. Using averages for this period: Z (the total mortality rate) was 1.1375, Z_n (the natural mortality rate) was 1.1351, and Z_f (the plant fishing mortality rate) was 0.0025.

SECTION 5

EXPERIMENTAL PROCEDURES

As mentioned earlier, impingement impacts owing to fish mortality at existing facilities are not readily assessed using conventional hypothesis testing techniques. The existing fish community "is what it is" under the operating regime of the facility. What it was or "would be" in the absence of the plant is not an observation normally available to the experimentalist.

The impact of impingement mortalities on fish populations can be manifested in three general ways or plateaus of impact. There may be: (1) no impact to the fish population if growth and survival mechanisms are sufficiently great to compensate impingement losses, (2) depression to some lower level of abundance where compensatory mechanisms resist further decreases, or (3) eventual extirpation of the fish population at some time. A fourth possibility exists at the community level. Fish species for which individuals are not normally impinged in numbers sufficiently high to adversely affect their own populations may interact with species which are adversely impacted by impingement. Community structure (e.g., predator-prey interactions) could thus be modified as large impingement losses for one species are translated through the fish community. This is a problem which cannot be addressed with a single species model such as developed here except in the trivial case where no impact to the population under study is predicted (where interacting populations are presumed also to be unaffected).

With these factors in mind, a model was constructed which utilized an estimated fishing mortality rate (i.e., the impingement rate) for Cumberland Steam-Electric Plant in conjunction with the natural mortality rate estimated for the gizzard shad population of Barkley Reservoir. This procedure, as a result of deliberately varying the fishing rate coefficient, was used to estimate the effects of the plant on the gizzard shad population as described below. However, it is important to note that these efforts do not represent experiments in the classical sense of hypothesis testing. Rather, they are hypothetical experiments which are beyond the ability of the investigators to perform and for which a model has been developed to predict outcomes.

BASELINE CONDITIONS

The term "baseline conditions" as used here refers to the population as it exists with operation of the plant. This was accomplished by first running the model with the mortality coefficients applicable for the gizzard shad population as it exists with the operating plant. This provided a reference with which to make assessments considering other operational regimes for the platn.

ZERO PLANT MORTALITY

In this scheme, the model was run with the plant fishing mortality coefficient set equal to zero. Thus, the gizzard shad population predicted by the model is that expected for Barkley Reservoir if Cumberland Steam-Electric Plant was not present or if impingement mitigation was undertaken and 100 percent effective. The difference between the zero mortality and baseline condition estimates is the predicted impact of the plant on the gizzard shad population.

TEN-FOLD MORTALITY INCREASE

For this experiment, the plant was assumed to impinge 10 times as many gizzard as are presently estimated to be killed, with other baseline parameters unchanged. This is roughly equivalent to siting a similar facility on a lake one-tenth the size of Barkley Reservoir or, increasing plant size by a factor of 10. This translates into about 0.9 MWe/ha, a normal ratio for cooling ponds but considerably lower than ratios for plants located on multipurpose reservoirs. Plant intake volume would be about 10 percent of the reservoir per day. The prediction obtained in this case perhaps reflects the impact of impingement alone to gizzard shad populations in cooling ponds.

ONE-HUNDRED-FOLD MORTALITY INCREASE

This experimental run was similar to the previous test except that the plant was assumed to impinge 100 times as many gizzard shad as are currently estimated to be killed. Plant-to-reservoir ratios in this case were 9 MWe/ha with a daily intake volume equivalent to 97 percent of the reservoir volume. These ratios are not approached for plants located on reservoirs and are rarely found in flowing streams, and then usually for only a small portion of the year.

SECTION 6

RESULTS AND DISCUSSION

The total numbers of fish in the cohort and cohort length distributions were first simulated for baseline or current conditions at yearly intervals (Table 7). The total numbers of fish simulated by the model for the first year of life were generally very similar to cove rotenone sample estimates (Figure 24). Simulated second- and third-year numbers were somewhat lower than the actual measured numbers, while fourth-year model predictions were very close to the numbers observed.

The model also predicted changes in the length distribution through time. The predicted length distributions followed the same pattern as the observed size distribution; that is, they become narrower through time. This phenomenon is expected if the growth rate is decreasing as a function of length (see DeAngelis and Mattice 1979, Bodola 1965, Ricker 1975), and is known as compensatory growth. The model length distributions tended to be narrower than the observed distribution (Figure 25). Despite these differences in the variances of the length distributions between the model and observations, the mean length at the end of each year predicted by the model was close to that observed except in the case of age IV. This is easily explained by the fact that there was only a single individual of age IV sampled (see Materials and Methods section).

The differences in the variances of the real and simulated size distributions are probably due to the fact that there is a great deal of heterogeneity within the actual population (i.e., differences in growth rates among individuals due to genetic and environmental variability) that was not incorporated in the simulation shown in Figure 25. However, the model is structured to permit inclusion of these differences within the cohort in an approximate way by allowing division of the cohort into a number (up to 20) of subcohorts, each with its own growth rate $G_i(s,t)$. Because of this poor fit, a simulation was made in which the cohort was divided into nine subcohorts, distributed roughly normally about the mean growth rate, ranging from 0.6 to 1.4 of the mean value. The results of this simulation are shown in Figure 26, where the numbers are the sums over the subcohorts, these sums being the discrete approximation to Eq. (A.49) in the appendix. Note that the spread in growth rates has resulted in an increase in variance of the simulated size distribution so that it more closely approximates the observed distribution. Since there is little available information on the true spread in growth rates within a cohort, these results can only be viewed as indicative.

The model was next run with plant mortality set equal to zero. Estimated total numbers differed by less than 1.0 percent from the baseline case for every age class and length distributions were identical in appearance for the two cases. These results indicate that the effect of the plant on a gizzard shad cohort is negligible.

TABLE 7. LENGTH FREQUENCY OF GIZZARD SHAD IN COVE ROTENONE SAMPLES BY AGE CLASS COMPARED WITH THE RESULTS OF SIMULATIONS RUN UNDER FOUR TEST CASES

	Length Group					
	25-49	50-74	75-99	100-124	125-149	150-174
COVE ROTENONE SAMPLES						
Age 0	249.550	6017.150	2365.500	704.600	700.350	140.580
Age I				70.50	1006.750	851.500
Age II						14.910
Age III						
Age IV						
BASELINE CONDITIONS						
INITIAL	249.550	6017.150	2365.500	704.600	700.350	140.580
Age I						3014.121
Age II						
Age III						
Age IV						
ZERO PLANT MORTALITY						
INITIAL	249.550	6017.150	2365.500	704.600	700.350	104.580
Age I						3021.291
Age II						
Age III						
Age IV						
TEN-FOLD INCREASE						
INITIAL	249.55	6017.15	2365.50	704.60	704.35	104.58
Age I						2953.860
Age II						
Age III						
Age IV						
ONE-HUNDRED-FOLD INCREASE						
INITIAL	249.550	6017.150	2365.500	704.600	704.350	104.580
Age I						2271.787
Age II						
Age III						
Age IV						

TABLE 7. (Continued)

	Length Group					
	175-199	200-224	225-249	250-274	275-299	300-324
COVE ROTENONE SAMPLES						
Age 0						
Age I	971.380	485.580	14.180			
Age II	220.770	282.160	60.570	2.120	0.180	
Age III		6.560	5.150	3.180	0.520	0.100
Age IV						0.100
BASELINE CONDITIONS						
INITIAL						
Age I	590.572	11.300				
Age II		198.835	1.538			
Age III			4.203	0.010		
Age IV				0.095		
ZERO PLANT MORTALITY						
INITIAL						
Age I	591.977	11.327				
Age II		199.782	1.546			
Age III			4.233	0.010		
Age IV				0.096		
TEN-FOLD INCREASE						
INITIAL						
Age I	578.765	11.074				
Age II		190.964	1.477			
Age III			3.956	0.010		
Age IV				0.087		
ONE-HUNDRED-FOLD INCREASE						
INITIAL						
Age I	445.122	8.517				
Age II		112.955	0.874			
Age III			1.800	0.004		
Age IV				0.031		

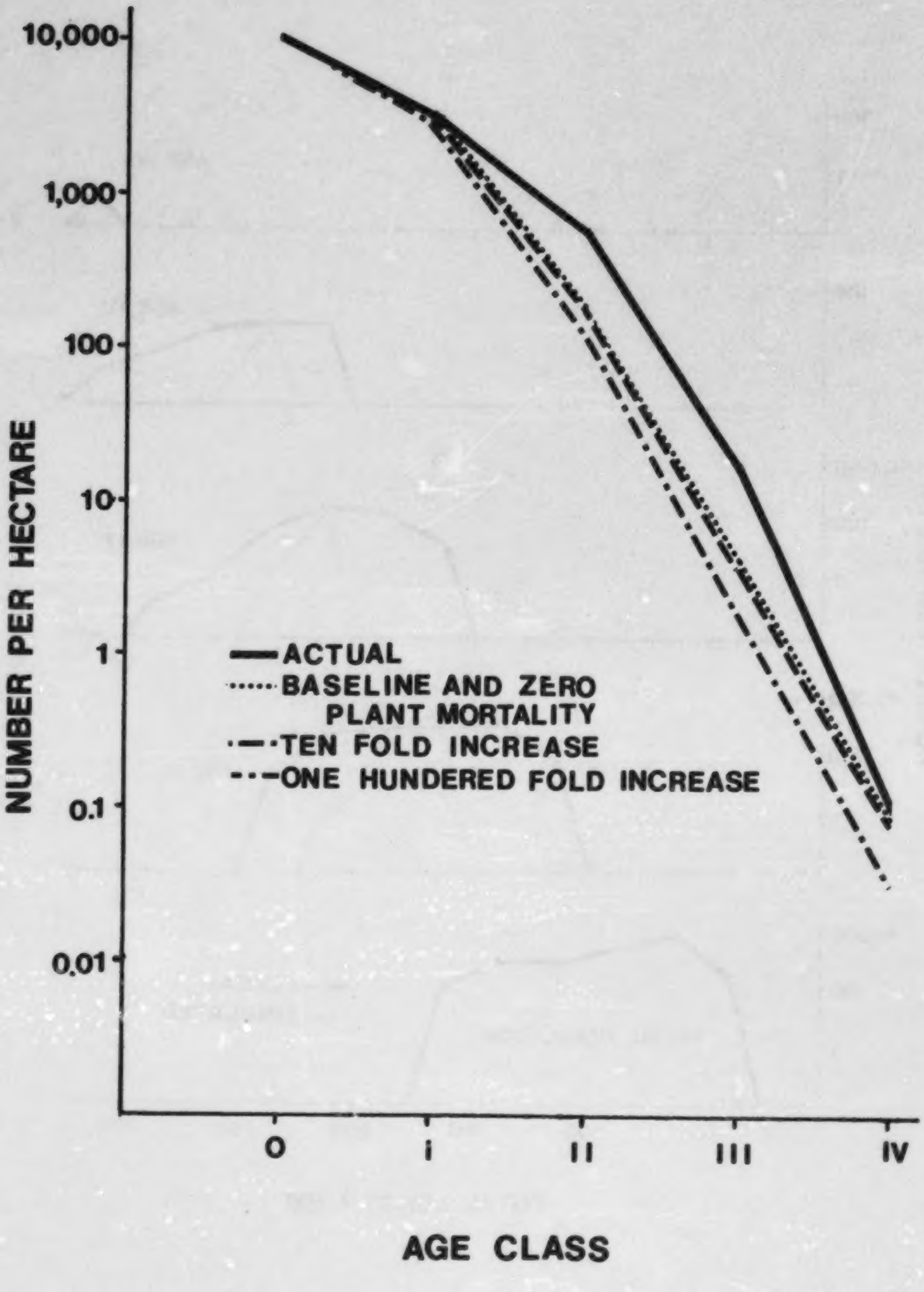

Figure 24. Comparison of age structure in cove rotenone samples with results of simulations run under four test cases (simulated populations under baseline and zero plant mortality situations are represented by the same line).

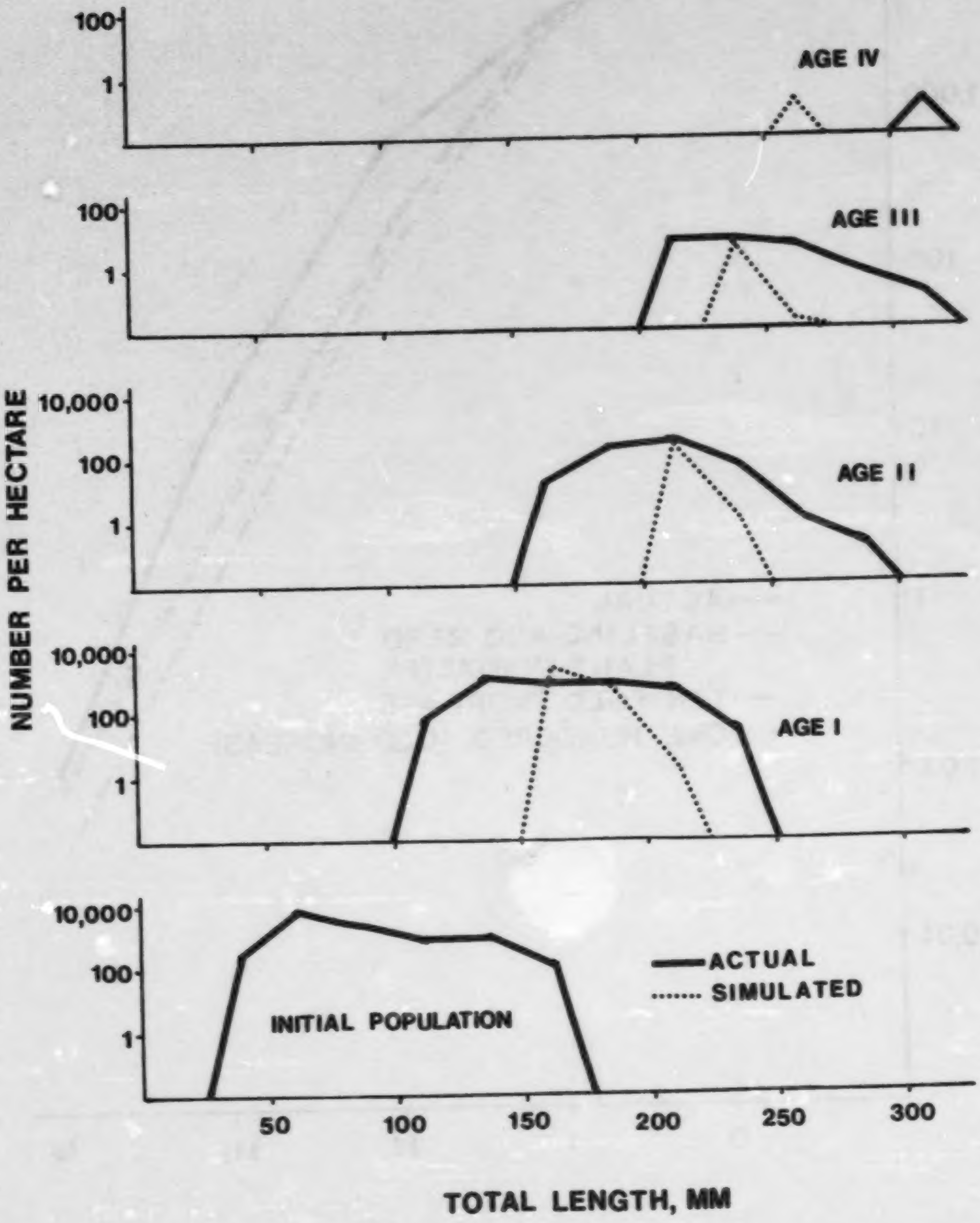

Figure 25. Length frequencies simulated using baseline conditions compared with cove rotenone estimates.

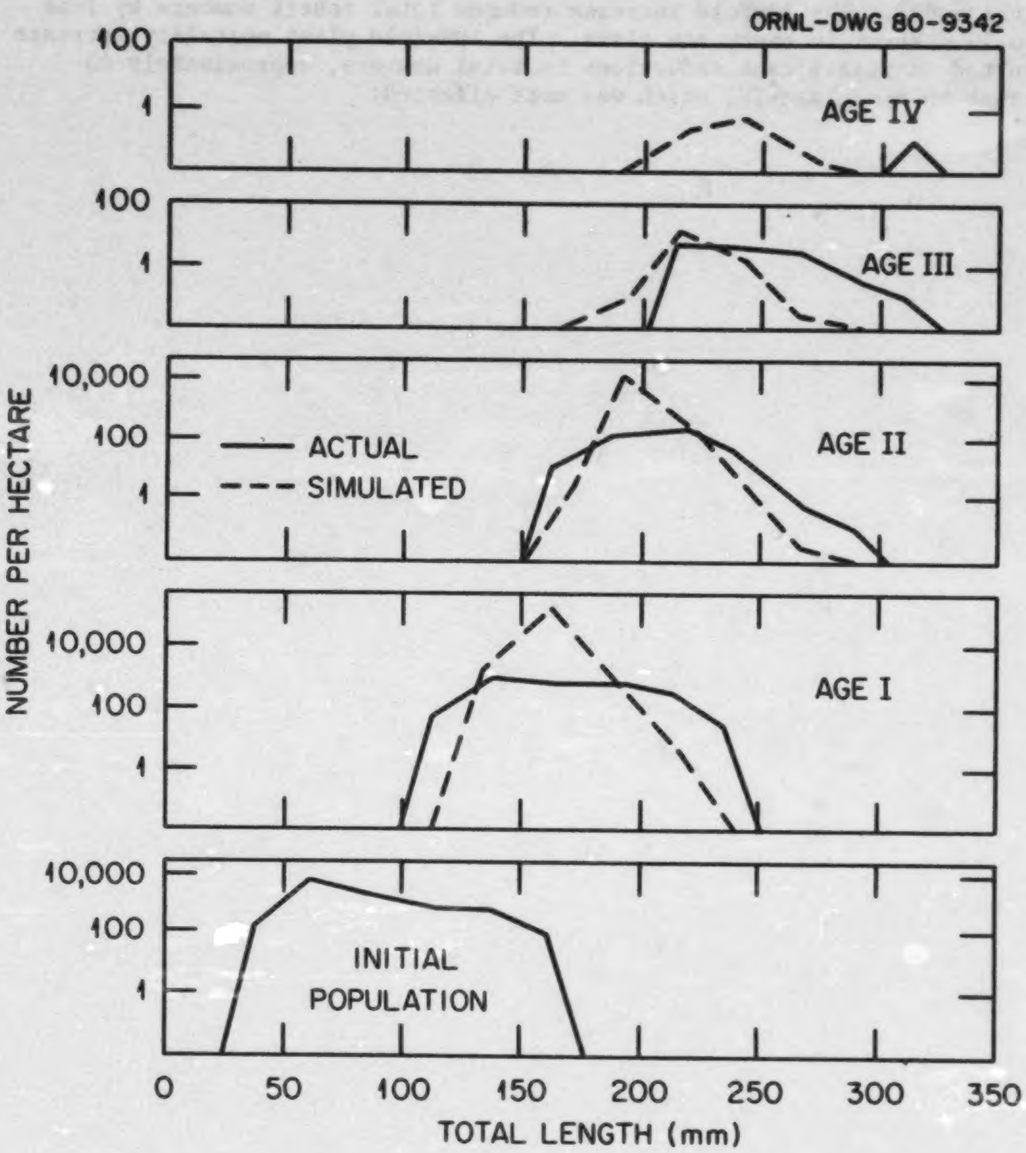

Figure 26. Length frequencies of the simulation in which the cohort is divided into nine subcohorts with different growth rates using baseline conditions, compared with cove rotenone estimates.

Next, 10- and 100-fold plant mortality rates increases were assumed in the model. The 10-fold increase reduced total cohort numbers by less than 10 percent in every age class. The 100-fold plant mortality increase resulted in significant reductions in total numbers, approximately 65 percent in age class IV, which was most affected.

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APPENDIX A: ANALYSIS OF MODEL

1. Solution of the partial differential equation for time-invariant growth and mortality rates

Solution of Eq. (11) is obtainable by the method of characteristics. See, for example, Hildebrand (1962), Courant and Hilbert (1966), or Van Sickle (1977). To apply this method, it is easiest to first make the further assumptions that $G(s,t) = G(s)$ and $Z(s,t) = Z(s)$ and that all recently hatched fish have the same size $s = s_0$. Then $B(s,t)$ can be written

$$B(s,t) = B_0(t)\delta(s-s_0) \ , \tag{A.1}$$

where $\delta(s-s_0)$ is the Dirac delta-function, defined by the properties

$$\delta(s-s_0) = 0 \text{ for } s \neq s_0 \tag{A.2}$$

$$\int_{s_a}^{s_b} \delta(s-s_0)f(s)ds = f(s_0) \text{ for } (s_a < s_0 < s_b) \ , \tag{A.3}$$

where $f(s)$ is an arbitrary function. The Dirac delta-function may be visualized as a very sharp spike at $s=s_0$, having unit area.

The replacement of $B(s,t)$ by $B_0(t)\delta(s-s_0)$ reduces Eq. (11) to

$$\frac{\partial N(s,t)}{\partial t} + \frac{\partial}{\partial s}\{G(s)N(s,t)\} = -Z(s)N(s,t) + B_0(t)\delta(s-s_0) \tag{A.4}$$

or

$$\frac{\partial N(s,t)}{\partial t} + G(s)\frac{\partial N(s,t)}{\partial s} = -\{Z(s) + \frac{\partial G(s)}{\partial s}\}N(s,t) + B_0(t)\delta(s-s_0) \tag{A.5}$$

To determine the boundary condition, integrate both sides of Eq (A.4) over a very small region surrounding $s=s_0$;

$$\int_{s_0 - \frac{\varepsilon}{2}}^{s_0 + \frac{\varepsilon}{2}} \left[\frac{\partial N(s,t)}{\partial t} + \frac{\partial}{\partial s}\{G(s)N(s,t)\} + Z(s)N(s,t) - B_0(t)\delta(s-s_0)\right] ds = 0 \ . \tag{A.6}$$

Thus, taking each term in (A.6), the following results are obtained:

$$\int_{s_0 - \frac{\varepsilon}{2}}^{s_0 + \frac{\varepsilon}{2}} \frac{\partial N(s,t)}{\partial N} \, ds \cong \varepsilon \; \frac{\partial N(s_0,t)}{\partial t} \underset{\varepsilon \;\; 0}{=} 0 \tag{A.7}$$

$$\int_{s_0 - \frac{\varepsilon}{2}}^{s_0 + \frac{\varepsilon}{2}} \frac{\partial}{\partial s} \{G(s)N(s,t)\} \, ds = G(s)N(s,t) \Bigg|_{s_0 + \frac{\varepsilon}{2}}^{s_0 + \frac{\varepsilon}{2}} \tag{A.8}$$

$$\underset{\varepsilon \;\; 0}{\cong} G(s_0)N(s_0,t)$$

$$\int_{s_0 - \frac{\varepsilon}{2}}^{s_0 + \frac{\varepsilon}{2}} Z(s)N(s,t) \, ds \cong \varepsilon Z(s_0)N(s_0,5) \underset{\varepsilon \;\; 0}{\rightarrow} 0 \tag{A.9}$$

$$\int_{s_0 - \frac{\varepsilon}{2}}^{s_0 + \frac{\varepsilon}{2}} B_0(t)\delta(s-s_0) \, ds = B_0(t) \tag{A.10}$$

The result (A.8) follows since it is assumed that $N(s,t) = 0$ for all $s < s_0$. See Eq. (A.3) for the derivation of (A.10). Therefore, using these results in Eq. (A.6), the boundary conditions on $N(s,t)$ are found to be

$$N(s_0,t) = B_0(t)/G(s_0). \tag{A.11}$$

The theory of partial differential equations (e.g., Hildebrand 1962) implies that the general solution of Eq. (A.5) is of the form $F(u_1,u_2) = 0$, where $F(u_1,u_2)$ is any function relating u_1 and u_2, and where $u_1(N,s,t) = C_1$ and $u_2(N,s,t) = C_2$ are solutions of any two differential equations that imply

$$\frac{dt}{1} = \frac{ds}{G(s)} = \frac{-dN}{\{Z(s) + \frac{dG(s)}{ds}\} N} , \tag{A.12}$$

where C_1 and C_2 are constants of integration.

In the present case, in which boundary conditions are posed on the $s = s_0$ plane, it is convenient to choose to integrate the equations formed by terms 1 and 2 and by terms 2 and 3. Performing the integrations, there result

$$u_1(N,s,t,) = t - I(s_0,s) = C_1 \tag{A.13}$$

and

$$u_2(N,s,t) = \ln(N) + \ln \{G(s)/G(s_0)\} + J(s_0,s) = \ln(C_2), \tag{A.14}$$

where

$$I(s_0,s) = \int_{s_0}^{s} \frac{ds'}{G(s')} \tag{A.15}$$

and

$$J(s_0,s) = \int_{s_0}^{s} \frac{Z(s')\,ds'}{G(s')} . \tag{A.16}$$

Equations (A.13) and (A.14) can be expressed as

$$t = I(s_0,s) + C_1 \tag{A.17}$$

and

$$N = C_2\{\frac{G(s_0)}{G(s)}\}\, e^{-J(s_0,s)} . \tag{A.18}$$

These two equations each define a family of integral surfaces in (N,s,t)-space (Fig. A.1). The intersection of a given pair of surfaces from these families defines a curve called the characteristic curve.

What is now necessary is to specify the particular solution in the relation $F(u_1,u_2) = 0$, or, equivalently, $F(C_1,C_2) = 0$. This relation must be such that the boundary value condition, Eq. (A.11), is satisfied. Choose as $F(C_1,C_2)$ the equation

$$C_2 = B_0\{C_1\}/G(s_0) , \tag{A.19}$$

or, from Eq. (A.17),

$$C_2 = B_0\{t - I(s_0,s)\}/G(s_0) . \tag{A.20}$$

It can be seen from Eq. (A.18) that, using this assumption, the particular solution is

$$N(s,t) = \frac{B_0\{t - I(s_0,s)\}e^{-J(s_0,s)}}{G(s)} , \tag{A.21}$$

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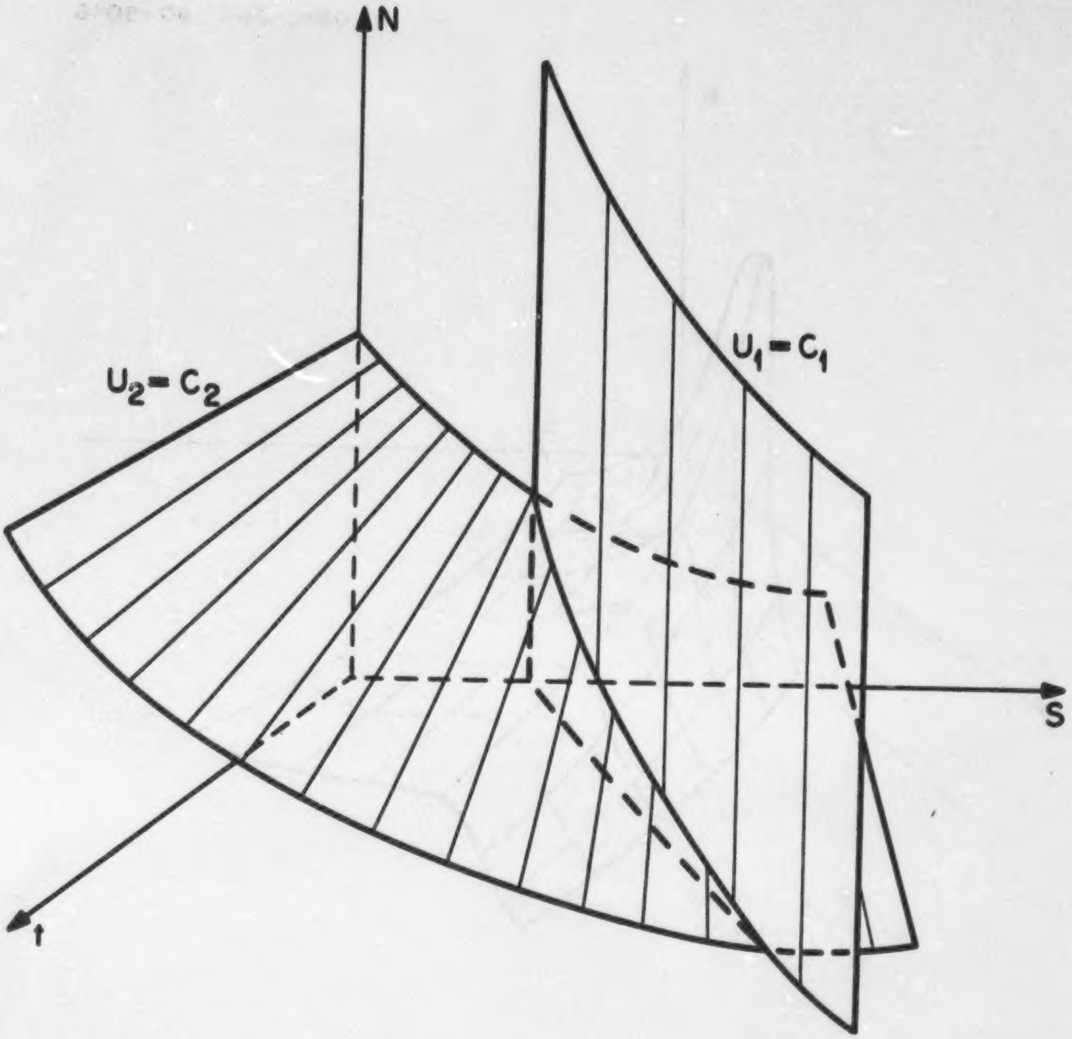
N
$U_2 = C_2$
$U_1 = C_1$
S
t

Figure A.1. The integral surfaces defined by Eqs. (1-17) and (A.18). The intersection of these surfaces is the characteristic curve.

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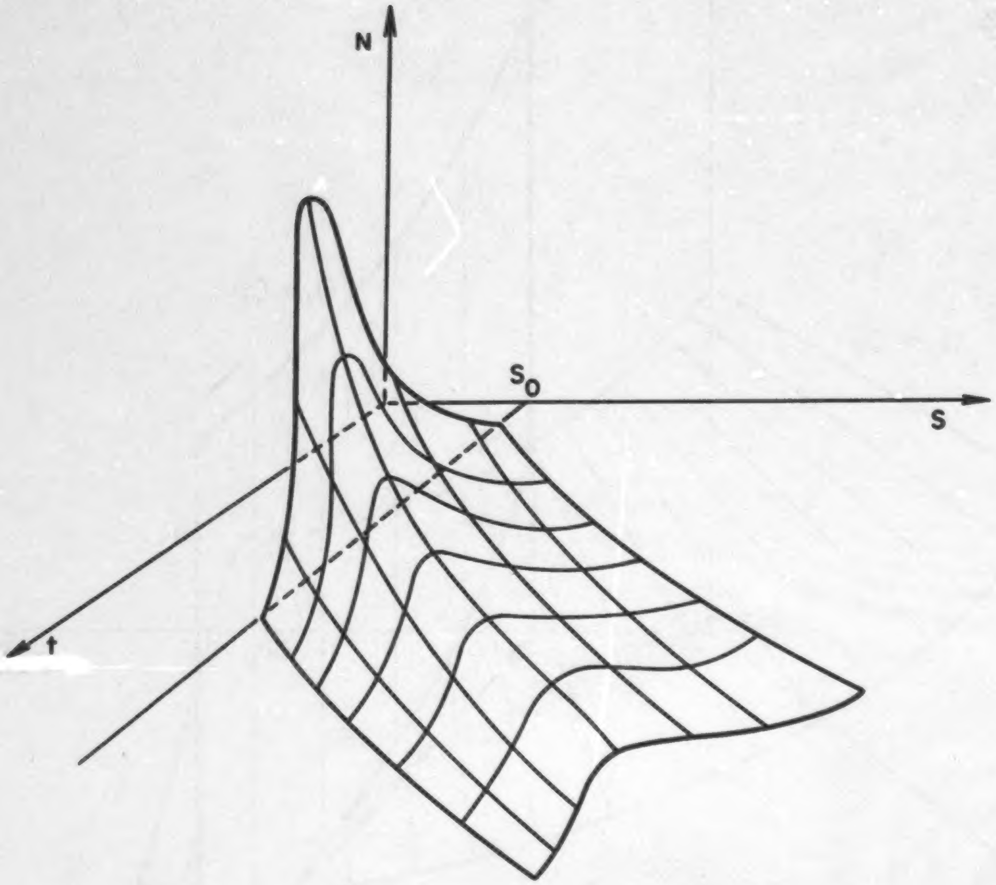

Figure A.2. The surface N(s,t) as defined by Eq. (A.21). It is composed of characteristic curves.

(Fig. A.2). The surface defined by Eq. (A.21) is composed of characteristic curves satisfying Eq. (A.19). It can be seen that for $s = s_0$, $N(s,t) = B_0(t)/G(s_0)$.

The simplicity of the above analytic solution hinges on the time invariance of G(s) and Z(s) and on the approximation (A.1) for B(s,t). Cases where these assumptions need not hold will be considered later.

2. Particular solutions of the equation

Any attempt to model empirical data requires that specific forms of G(s), Z(s), and $B_0(t)$ be used. Fortunately, G(s) can often be approximated by very simple functions. Two cases are given below.

Case 1

The early growth of many fish is approximately exponential. Hence,

$$G(s) = g_0 s \ , \tag{A.22}$$

where g_0 is a constant. If the mortality rate, Z(s), is assumed to be constant, Z_0, then $I(s_0,s)$ and $J(s_0,s)$ become

$$I(s_0,s) = \int_{s_0}^{s} \frac{ds'}{g_0 s'} = \frac{1}{g_0} \ln(s/s_0) \tag{A.23}$$

$$J(s_0,s) = \int_{s_0}^{s} \frac{ds' Z_0}{g_0 s} = \frac{Z_0}{g_0} \ln(s/s_0) \tag{A.24}$$

Equation (A.21) then becomes

$$N(s,t) = \frac{B_0\{t - (1/g_0)\ln(s/s_0)\}}{g_0 s} \exp\{- \frac{Z_0}{g_0} \ln(s/s_0)\}$$

$$= \frac{B_0\{t - (1/g_0)\ln(s/s_0)\}}{g_0 s} \left(\frac{s}{s_0}\right)^{-(Z_0/g_0)} \tag{A.25}$$

Some discussion of the meaning of this expression may be helpful at this point. First, to interpret $B_0\{t - (1/g_0)\ln(s/s_0)\}$, recall that $B_0(t)$

is reproduction as a function of time. For most fish species of interest, spawning is confined to a relatively short period of time during the year, perhaps a few weeks. Denote by $T_0 = 0$ the beginning of the spawning period and the end by T_s. Over this period, B(t) will have some distribution, which can perhaps be very crudely approximated by a truncated normal distribution (Fig. A.3).

The expression $B_0\{t - (1/g_0)\ln(s/s_0)\}$ in Eq. (A.25), however, is a function of $t - (1/g_0)\ln(s/s_0)$, and hence of both t and s. Consider this expression from two points of view. First, consider $B_0\{t - (1/g_0)\ln(s/s_0)\}$ as a function of time for various values, s_i, of s ($s_i \geq s_0$). Several such curves are plotted in Fig. A.4. Note that as s_i increases, the curve moves to the right. If t_i signifies the time when cohort members first reach size s_i, then note that as s_i increases, the time interval between successive values of times, t_i and t_{i+1}, decreases since growth is accelerating.

One can also consider the expression $B_0\{t - (1/g_0)\ln(s/s_0)\}$ from the standpoint of variation with respect to s at fixed times, $t_1, t_2, \ldots, t_n$ (Fig. A.5). Each curve is the size distribution for the particular associated time, t_i. Note that the size distribution spreads through time since the ratio of the upper to lower limits, s_{up}/s_{low}, is

$$\frac{s_{up}}{s_{low}} = \exp(g_0 T_s) \ . \tag{A.26}$$

In Fig. A.5, $B_0\{t - (1/g_0)\ln(s/s_0)\}$ has been divided by $g_0 s$, as in Eq. (A.25), so that in the absence of mortality ($Z_0 = 0$), population number is conserved; i.e., it can be shown by a change of variable that

$$\int_{s_{low}}^{s_{up}} \frac{B_0\{t - (1/g_0)\ln(s/s_0)\}}{g_0 s}\, ds = \int_0^{T_s} B_0(x)\, dx \tag{A.27}$$

for all values of t. The factor $(s/s_0)^{-(Z_0/g_0)}$ in Eq. (A.25) is a quantity between 0 and 1.0, representing the fraction of surviving fish.

Case 2

Growth characteristics for individual organisms of many species have the appearance of logistic curves when examined over the total life spans;

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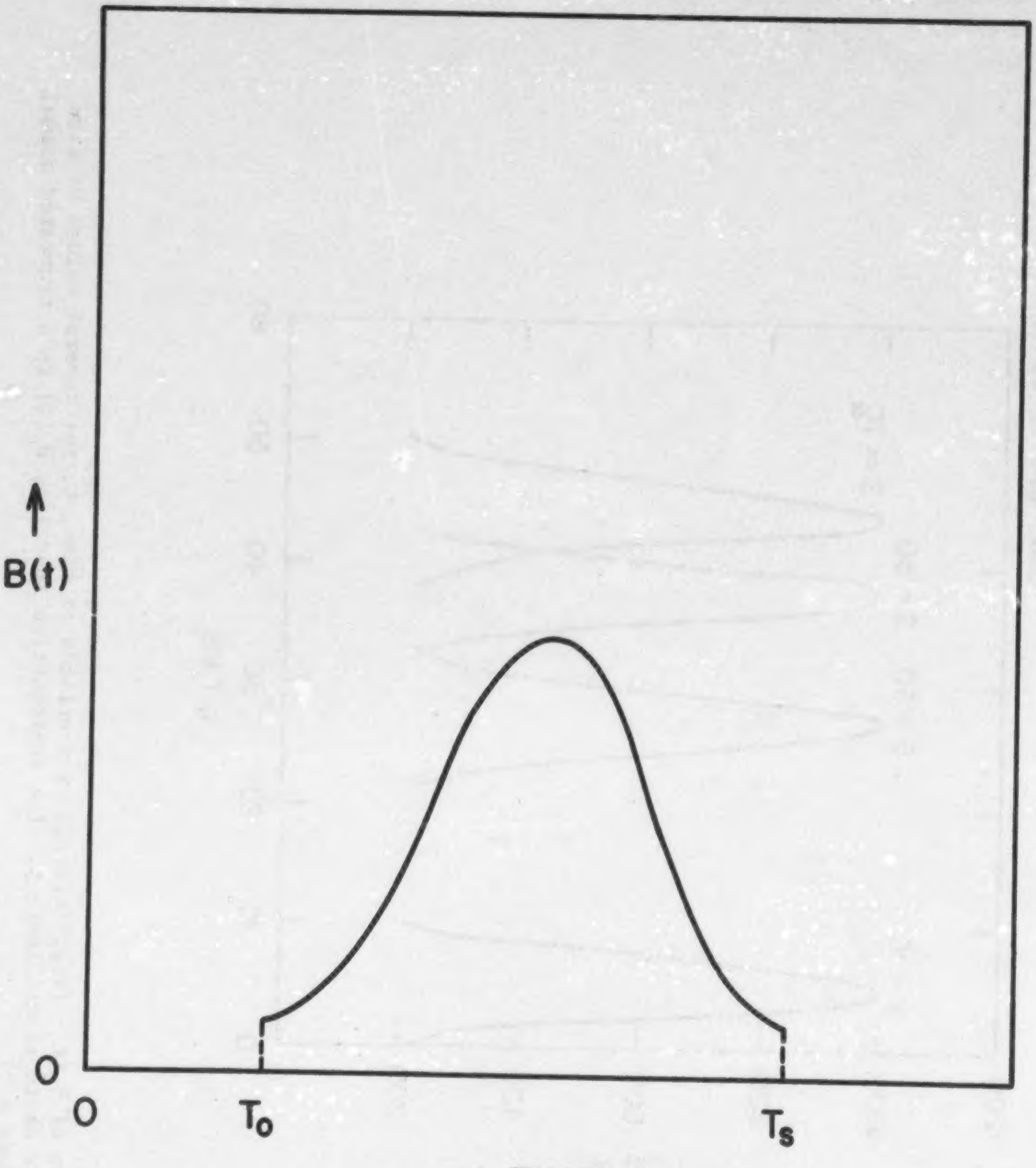

Figure A.3. A hypothetical recruitment rate, B(t), between the times $t=0$ and $t=T_s$.

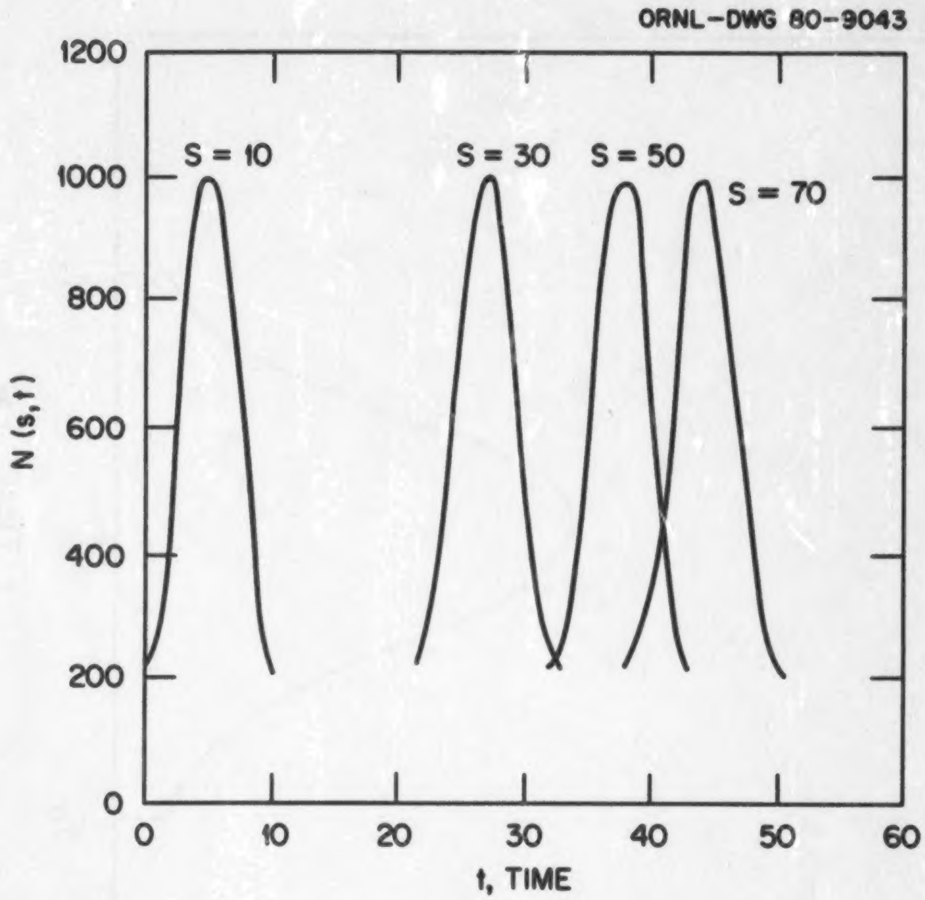

Figure A.4. Plots of $B_0\{t - (1/g_0)\ln(s/s_0\}$ as functions of time, t, for several values of size, s, in units of millimeters. The reproduction function, $B_0(t)$ is a truncated normal (Figure A.3).

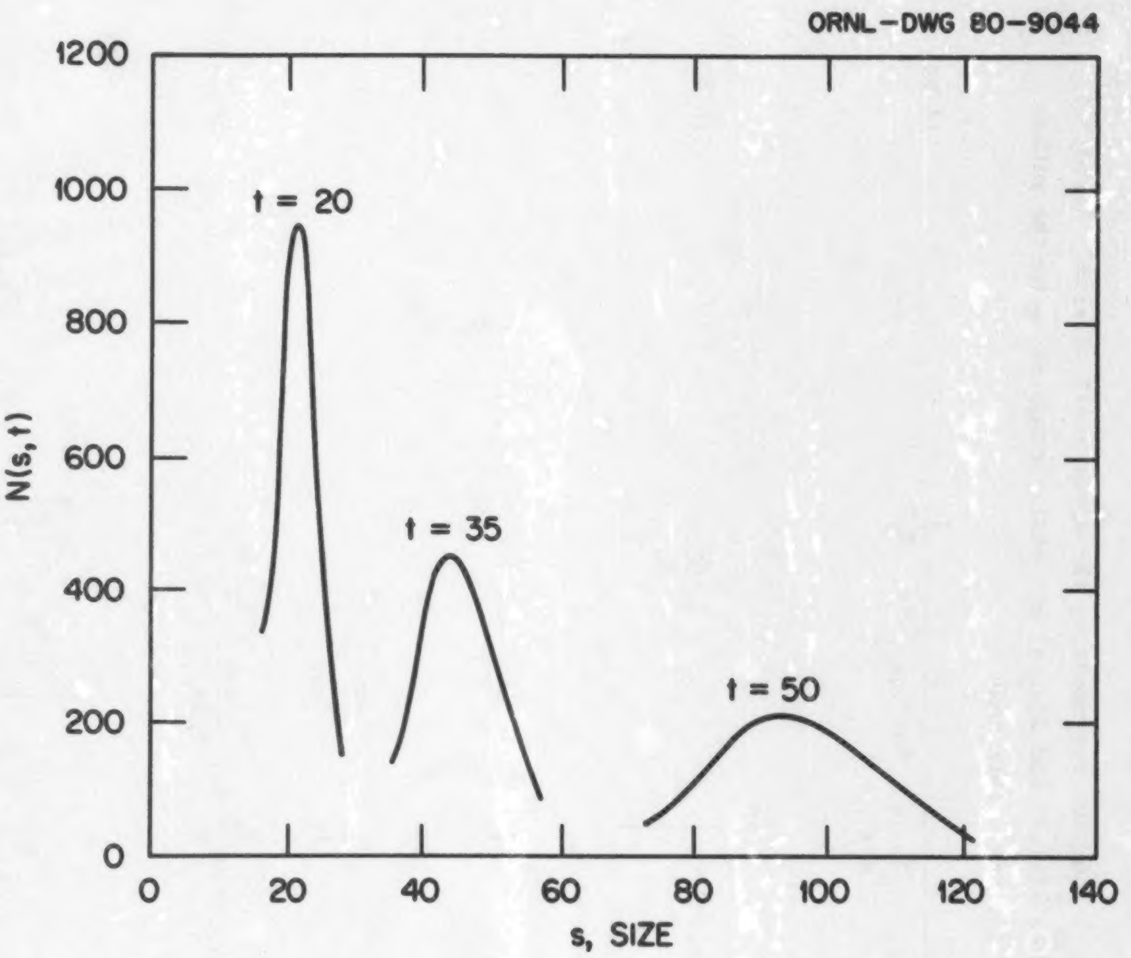

Figure A.5. $B_0\{t - (1/g_0)\ln(s/s_0)\}/g_0 s)$ as function of size, s, for three values of time, t. The reproductive function, $B_0(t)$, is a truncated normal (Fig. A.3).

some examples are given by DeAngelis and Mattice (1979). Early growth in the life span is approximately exponential, but later slows down and eventually plateaus. Growth rate in these cases can be approximated by the function

$$G(s) = g_0(1 - \frac{s}{s_{max}})s \ , \qquad (A.28)$$

where s_{max} is a constant representing the upper limit of size. Again, if $Z(s) = Z_0$, then $I(s_0,s)$ and $J(s_0,s)$ are easily computed using the method of partial fractions. Note that

$$\frac{1}{g_0(1 - \frac{s}{s_{max}})s} = \frac{1}{g_0(s_{max} - s)} + \frac{1}{g_0 s} \ , \qquad (A.29)$$

so that

$$I(s_0,s) = \int_{s_0}^{s} (\frac{1}{s_{max} - s} + \frac{1}{s}) \frac{ds'}{g_0} \qquad (A.30)$$

$$= \{ - \frac{1}{g_0} \ln(s_{max} - s') + \frac{1}{g_0} \ln(s')\} \Bigg|_{s_0}^{s}$$

$$= \frac{1}{g_0} \ln \frac{s(s_{max} - s_0)}{s_0(s_{max} - s)}$$

$$J(s_0,s) = \frac{Z_0}{g_0} \ln\{ \frac{s(s_{max} - s_0)}{s_0(s_{max} - s)} \} \qquad (A.31)$$

Then

$$N(s,t) = \frac{s_{max}}{g_0(s_{max} - s)s} \left[\frac{s_0(s_{max} - s)}{s(s_{max} - s_0)}\right]^{Z_0/g_0} B\{t - I(s_0 s)\} \qquad (A.32)$$

The size distribution, N(s,t) exhibits interesting behavior. Assume that B(t) has a truncated normal distribution,

$$B(t) = \begin{cases} 0 & t < 0 \\ b_0 \exp -(t - 0.5T_s)^2/b_1^2 & 0 \le t \le T_s \\ 0 & T_s < t \end{cases} \qquad (A.33)$$

where b_0 and b_1 are constants. In Fig. A.6 the size distribution of the cohort is computed for several values of t and for a set of hypothetical parameter values. In this example, Z_0 is assumed to be zero for all values of s, so N(s,t) is given by Eq. (A.32) with $Z_0 = 0$. Time is measured in years from initial production of the cohort. Note that unlike the preceding example, the initial broadening of the size distribution is followed by a narrowing through time (Fig. A.7). The mean size follows a logistic curve, as expected. The standard deviation increases at first, then asymptotes and finally decreases as the sizes of individuals in the cohort approach their upper limit.

The variations in standard deviation are somewhat unexpected but can easily be interpreted. In the initial phase of growth, when size is accelerating ($d^2s/dt^2 > 0$), the largest fish (those produced earliest) always grow at faster rates than smaller individuals, leading to a broadening of the size distribution. Later, when $d^2s/dt^2 < 0$, the smallest fish grow faster than the larger ones and tend to catch up in size, causing the size distribution to become narrower.

A rough mathematical interpretation for the occurrence of the peak in the standard deviation curves close to the point of the maximum growth rate can be made. The size distribution should be broadest in the region in which the argument of B, $t - I(s_0,s)$, changes most slowly with respect to s. For an increment in $I(s_0,s)$, $\Delta I(s_0,s) = \Delta s/G(s)$, the argument is least sensitive when G(s) attains its maximum value.

3. Generalization to time-varying coefficients

At best, Eqs. (A.22) and (A.28) may be reasonable approximations of the growth rate under special conditions. They will certainly not be good approximations when environmental parameters such as temperature and food availability change significantly over time scales of interest. Seasonal changes in temperature greatly influence growth rates. Hence, we can hardly expect the assumptions that $G(s,t) = G(s)$ and $Z(s,t) = Z(s)$ to be valid in real cases, so solutions developed in the preceding two sections are not sufficient.

Despite the insufficiency of Eq. (A.21) for describing cohort dynamics when mortality and growth rate are functions of time, it can be extended to approximate these cases. If Z(s,t) and G(s,t) change relatively slowly with respect to time, say on a scale of months, then Eq. (A.21) for N(s,t) may be valid over short periods of time. Solutions for these short time periods can then be pieced together.

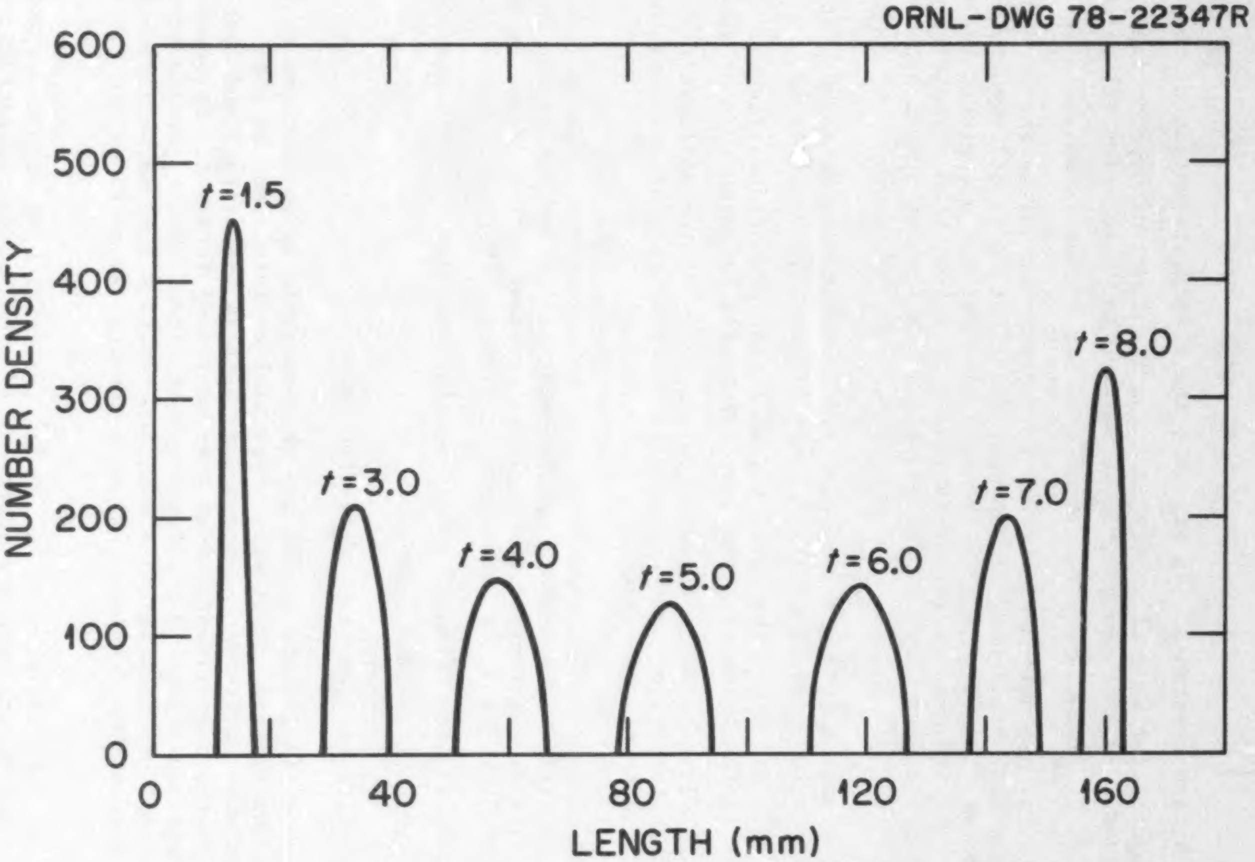

Figure A.6. N(s,t) from Eq. (A.32) as a function of size, s, for several values of time, t, and for arbitrarily chosen parameter values.

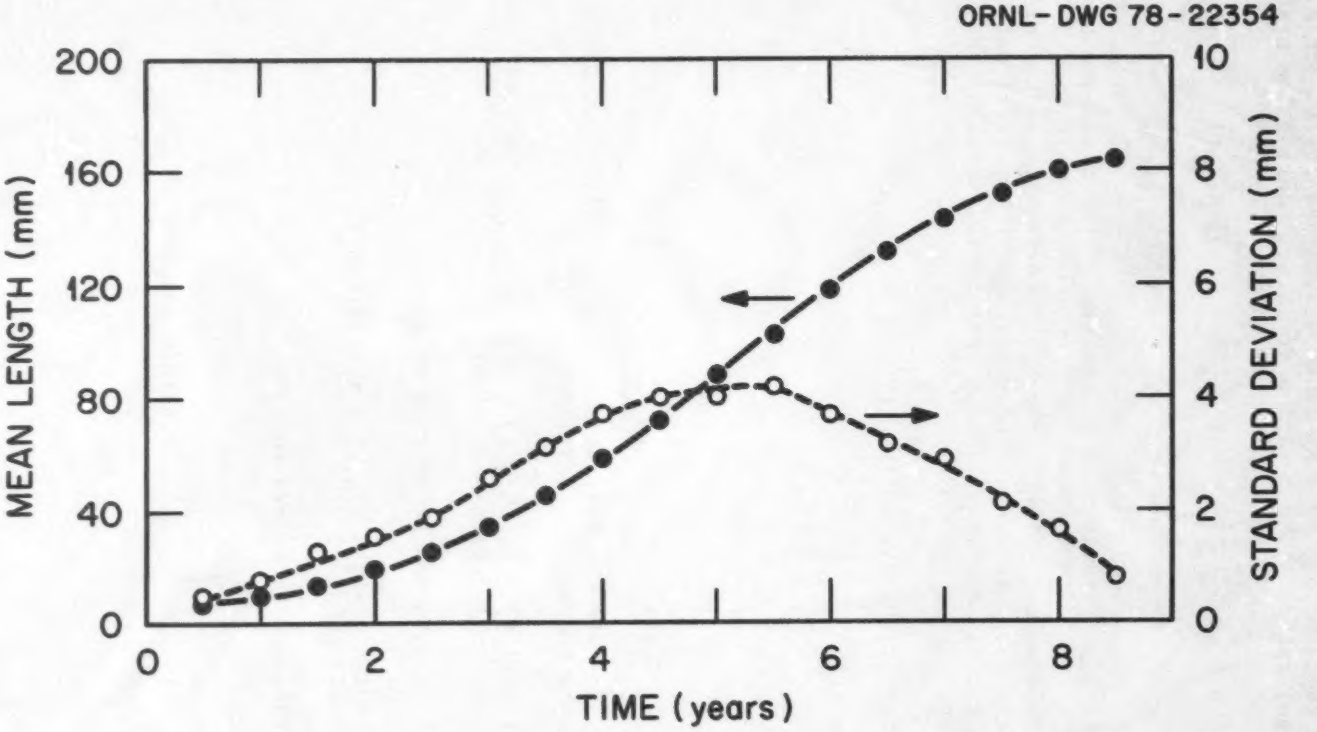

Figure A.7. The mean size in the cohort (black dots) and the standard deviation in size (white dots) as functions of time from Eq. (A.32). The parameter values have been chosen arbitrarily.

Assume that the spawning period has ended and that $N(s,t_i)$ has been computed for time t_i from Eq. (A.21). Assume that time t_i represents the end of one month and that during the next month $G(s,t)$ and $Z(s,t)$ are different from their original values. The equation for $N(s,t)$ during the next month is

$$\frac{\partial N(s,t)}{\partial t} + G(s)\,\frac{\partial N(s,t)}{\partial s} = -\left\{\frac{dG(s)}{ds} + Z(s)\right\} N(s,t) + N_0(s)\delta(t-t_i) \qquad \text{(A.34)}$$

where $N_0(s)$ is the size distribution at the end of the first month.

One can write down the solution for $N(s,t)$ using the method of characteristics. However, it is useful to go through an explicit, detailed solution for $N(s,t)$, since this will help keep better track of the mathematical steps.

Introduce the variable τ, defined by

$$\tau = t + I(s) \qquad \text{(A.35)}$$

where

$$I(s) \equiv \int^{s} \frac{ds'}{G(s')}$$

This substitution permits the left hand side of Eq. (A.34) to be written as a total derivative with respect to τ since

$$\frac{dN}{d\tau} = \frac{\partial t}{\partial \tau}\frac{\partial N(s,t)}{\partial t} + \frac{\partial s}{\partial \tau}\frac{\partial N(s,t)}{\partial s} = \frac{\partial N(s,t)}{\partial t} + G(s)\,\frac{\partial N(s,t)}{\partial s}\ . \qquad \text{(A.36)}$$

Therefore, Eq. (A.34) can now be written as

$$\frac{dN}{d\tau} = -\left\{\frac{dG(s)}{ds} + Z(s)\right\} N(s,t) + N_0(s)\delta(t-t_i). \qquad \text{(A.37)}$$

Equation (A.36) can be solved to give

$$N(s,t) = e^{-R(\tau)} \int^{t} e^{R(\tau')} N_0(s)\delta(t - t_i)\, d\tau' \qquad \text{(A.38)}$$

where

$$R(\tau) \equiv \int^{t} \left\{Z(s) + \frac{dG(s)}{ds}\right\} d\tau'\ . \qquad \text{(A.39)}$$

In Eqs. (A.38) and (A.39), s and t must be expressed in terms of τ using Eq. (A.35). In general, an explicit analytic expression for s in terms of τ is not possible since I(s) will not always be integrable analytically. Therefore, it may be necessary to obtain s in terms of τ numerically from Eq. (A.35), which we call s = F(τ - t). Equations (A.38) and (A.39) can be reexpressed as

$$N(s,t) = e^{-R(\tau)} \int^{t} e^{R(\tau')} N_0 F(\tau' - t)\delta\{\tau' - I(s) - t_i\}\, d\tau' \quad (A.40)$$

and

$$R(t) = \int^{t} \left\{ Z\{F(\tau' - t)\} + \frac{dG\{F(\tau' - t)\}}{ds} \right\} d\tau' \ . \quad (A.41)$$

Equation (A.40) integrates to

$$N(s,t) = \frac{G\{F(t_i + I(s) - t)\}}{G(s)}\, e^{-Q\{t_i + I(s),\, t + I(s)\}} \times N_0\{F(t_i + I(s) - t)\} \quad (A.42)$$

where

$$Q\{t_i + I(s), t + I(s)\} = \int_{t_i + I(s)}^{t + I(s)} \left\{ Z\{F(\tau' - t)\} \right\} d\tau' \quad (A.43)$$

Special case

Consider the special case where

$$G(s) = v\left(1 - \frac{s}{s_{max}}\right) s \qquad \text{and}$$

$$Z(s) = Z_0$$

In this case, I(s) has an analytic form,

$$I(s) = \frac{1}{v} \ln\left(\frac{s}{s_{max} - s}\right)$$

as does $F\{I(s) + t_i - t\}$,

$$F\{I(s) + t_i - t\} = \frac{s_{max}\, e^{v\,\{I(s) + t_i - t\}}}{1 + e^{v\{I(s) + t_i - t\}}}$$

$$= \frac{s\, s_{max}}{s + (s_{max} - s)e^{v(t-t_i)}} \; . \qquad \text{(A.44)}$$

$$R\{t_i + I(s),\, t + I(s)\} = -\,(Z_0 + v)(t - t_i) + 2\ \ln\,\{\,1 + \frac{s\, e^{-v(t\, -\, t_i)}}{s_{max} - s}\}.$$

$$-\ 2\ \ln\{1 + \frac{s}{s_{max} - s}\}$$

$$= -\,(v + Z_0)(t - t_i) - 2\ \ln\,\{\frac{(s_{max} - s) + s\, e^{-v(t\, -\, t_i)}}{s_{max}}\}\ . \qquad \text{(A.45)}$$

Finally, N(s,t) is

$$N(s,t) = e^{-(Z_0\, +\, v)(t\, -\, t_i)} \left\{ \frac{s_{max}}{(s_{max} - s) + s\, e^{-v(t\, -\, t_i)}} \right\}^2$$

$$\times\ N_0 \left\{ \frac{s_{max}\, s}{s + (s_{max} - s)\, e^{v(t\, -\, t_i)}} \right\} \qquad \text{(A.46)}$$

From Equation (A.42), N(s,t) can be calculated for all times in month i, up to time $t = t_{i+1}$. Then the size distribution, $N(s,t_{i+1})$ can be used as the new initial value function, $N_{i+1}(s)$, from which N(s,t) can be calculated for the succeeding month by the process outlined above.

4. Size-dependent mortality

The general formula for N(s,t) given by Eq. (A.21) and its extension to situations of time-varying mortality and growth rate in the preceding section should enable consideration of realistic populations. Of special interest in this report will be the influence of various types of mortality on cohort population number and length distribution.

It is useful to distinguish among the various types of mortality expected to occur; for example, between fishing mortality, $Z_f(s,t)$, and natural mortality, $Z_n(s,t)$. Natural mortality can itself be divided into different classes. Suppose the effects of a particular predator on the species being modeled are of interest. It will be useful to separate the mortality, $Z_{n1}(s,t)$, caused by this predator from the remaining natural mortality, $Z_{n,rem}(s,t)$.

What makes $Z_f(s,t)$ and $Z_{n1}(s,t)$ of interest is that these mortality sources are likely to act on restricted size class ranges. In particular, $Z_{n1}(s,t)$ will depend on the size ratios of predator to prey.

Assume, for example, that $Z_{n1}(s,t)$ has the form

$$Z_{n1}(s,t) = C_{pred}(s) \tag{A.47}$$

where

$$C_{pred}(t) = \int_{s_c}^{s_{max,p}} N_{pred}(s_p,t)\, C(s_p/s)\, ds_p, \tag{A.48}$$

where $N_{pred}(s_p,t)$ is the number of predators of size s_p, s_c is the maximum size at which a predator can devour a prey of length s, $s_{max,p}$ the maximum size of predators in the population, and $C(s_p/s)$ the likelihood of a predator of size s_p devouring a prey of size s in an encounter.

5. Distribution of parameter values

Another source of potential inaccuracy in the model is the assumption of certain types of uniformity in the cohort populations. For example, in the particular case for which N(s,t) is given by Eq. (A.32), the parameters s_0, S_{max}, and g_0 are treated as constants having the same values for every member of the population. This is an approximation, for certainly these parameters will differ for individual organisms due to both genetic and environmental variation. This variation can be taken into account in our model at the cost of some complication. Suppose for example that newly produced organisms do not all have the same growth rate coefficient, g_0, but that the sizes have some general distribution, $F(g_0)$. The size distribution, N(s,t), through time is given by

$$N(s,t) = \int_{g_0'}^{g_0''} F(g_0) N(s,t;g_0)\, dg_0 , \tag{A.49}$$

where g_0' and g_0'' are the lower and upper bounds, respectively, on the distribution of g_0, and $N(s,t;g_0)$ represents N(s,t) for a particular value of g_0. If Eq. (A.32) is the solution for N(s,t), and distribution functions are available for s_{max} and s_0 as well as for g_0, then one can generalize

Eq. (A.49) to a triple integral over the distribution functions for s_0, s_{max}, and g_0.

In general, one must use numerical methods to evaluate the integral (A.49). However, in some special cases the integral can be performed analytically, so that the effects of variation in a parameter value within the cohort can be investigated in more detail. For example, suppose all reproduction takes place close to a single instant, t=0, so that $B_0(t)$ can be approximated by $B_{00}\delta(t)$. Assuming $N(s,t)$ is given by Eq. (A.32) and also assuming that the parameters s_0, s_{max}, and g_0 do not (at this point) vary among the members of the cohort, then from

$$N(s,t) = \frac{s_{max}}{g_0(s_{max} - s)s} \left[\frac{s_0(s_{max} - s)}{s(s_{max} - s_0)}\right]^{Z_0/g_0} B_{00}\delta\{t - I(s_0,s)\} , \quad (A.50)$$

with $I(s_0,s)$ given by Eq. (A.28), the sizes of all surviving fish in the cohort will the the same at all times and be described by a logistic function.

The total number of fish, $N(t)$, at any time t is

$$N(t) = \int_{s'}^{s''} N(s,t)\, ds = B_{00}e^{-Z_0 t} , \quad (A.51)$$

where s' and s" are the upper and lower limits on sizes in the cohort at time t. This can be proven by substituting $N(s,t)$ given by Eq. (A.50) into the integral of Eq. (A.51) and integrating, after making the change of variable from s to u, where

$$u = t - I(s_0,s) = t - (1/g_0)\ln \left[\frac{s(s_{max} - s_0)}{s_0(s_{max} - s)}\right]. \quad (A.52)$$

Eliminating ds in favor of du by means of

$$ds = \frac{g_0 s_0 s_{max}(s_{max} - s_0)e^{g_0(u-t)}}{\{(s_{max} - s_0) + s_0 e^{g_0(u-t)}\}^2}\, du , \quad (A.53)$$

and then using

$$s = \frac{s_{max} s_0 e^{g_0(u-t)}}{(s_{max} - s_0) + s_0 e^{g_0(u-t)}} , \quad (A.54)$$

$$s_{max} - s = \frac{s_{max}(s_{max} - s_0)}{(s_{max} - s_0) + s_0 e^{g\,(u-t)}} , \tag{A.55}$$

and

$$\frac{s_0(s_{max} - s)}{s(s_{max} - s_0)} = e^{g_0(t-u)} . \tag{A.56}$$

the integral (A.51) becomes

$$\int_{u'}^{u''} du\; e^{Z_0(u-t)} B_{00}\delta(u) = B_{00}e^{-Z_0t} . \tag{A.57}$$

Now let one of the parameters, say g_0, have a normal distribution, $F(g_0)$, about the mean, $\bar{g}_0$;

$$F(g_0) = \frac{1}{(2\Pi)^{1/2}\beta} \exp \{ -(g_0 - \bar{g}_0)^2/2\beta^2 \} . \tag{A.58}$$

The size distribution, $N(s,t)$, can be calculated from

$$N(s,t) = \int_{\infty}^{\infty} N(s,t;g_0)F(g_0)\; dg_0 . \tag{A.59}$$

Substituting $N(s,t)$ from (A.50) and $F(g_0)$ from (A.58) into (A.59), and making a change of variables from g_0 to u using

$$u = t - \frac{1}{g_0} \ln(D) \tag{A.60}$$

$$du = - \frac{dg_0}{g_0^{\;2}} \ln(D) \tag{A.61}$$

where

$$D = \frac{s(s_{max} - s_0)}{s_0(s_{max} - s)} \tag{A.62}$$

it follows that

$$N(s,t) = \frac{B_{00}s_{max}}{(2\pi)^{1/2}\beta(s_{max} - s)s} \int_{-\infty}^{\infty} \frac{D^{-Z_0(t - u)/\ln(D)} \; e^{-\frac{\{\ln(D) - \bar{g}_0(t - u)\}^2}{2\beta^2(t - u)^2}} \; \delta(u)}{u - t} \, du \qquad (A.63)$$

or, using

$$D^{-Z_0 t/\ln(D)} = e^{-Z_0 t} , \qquad (A.64)$$

$$N(s,t) = \frac{B_{00}s_{max}e^{-\{\ln(D) - \bar{g}_0 t\}^2/(2\beta^2 t^2)} \; e^{-Z_0 t}}{(2\pi)^{1/2}b(s_{max} - s)st} . \qquad (A.65)$$

In a similar manner, it is possible to compute the size distribution, $N(s,t)$, given parameter distributions in either s_{max} or s_0.

6. Density-dependent growth rate

It is reasonable to expect that in sufficiently crowded populations the growth rate of individuals may be reduced because of food resource limitations. There are very few empirical data available on which to base models of density-dependent growth. Nonetheless, a simple relationship between the actual growth rate, $G'(s,t)$, the growth rate under uncrowded conditions, $G(s,t)$, and the total population size, $N_0(t)$ can be postulated;

$$G'(s,t) = G(s,t)/\{1.0 + \rho N_0(t)\} , \qquad (A.66)$$

where ρ is a constant coefficient.

APPENDIX B: USE OF THE COMPUTER PROGRAM

1. General information on the program

The purpose of the computer program is to solve the basic partial differential equation, Eq. (11), for the size distribution, N(s,t), through time. The growth rate, G(s,t), and the mortality rate, Z(s,t), depend on the size (e.g., length), s, and on the time of the year, t. The reproduction rate, B(s,t) = B(t), can be allowed to vary during the spawning period. The numerical formulas, Eqs. (A.21) and (A.42), are used to compute N(s,t). Note that GA(J), ZA(J), and BA(J) in the computer program correspond to discrete arrays of the mathematical variables G(s,t), Z(s,t), and B(t), respectively, in the text. To obtain G(s,t), Z(s,t), and B(t) from GA(J), ZA(J), and BA(J), interpolation is used; e.g.,

```
G(s,t) = GA(J) + (GA(J+1) + GA(J))*((s - SIZE(J))/(SIZE(J+1) - SIZE(J))),
```

where SIZE(J) < s < SIZE(J+1), and the array, GA(J), is assumed to represent the growth rate at size SIZE(J) at time t. (The array GA(J) can be reset at specified times as described below.)

Some simplifying assumptions are built into the program in its present form to keep it from becoming too complex. One of the main simplifications is that the temporal variations in GA(J) and ZA(J) are assumed to be discontinuous rather than smooth. For example, GA(J) for a particular month (or whatever time period is chosen) will be constant in time during the whole month (through varying with s, or the computer variable J), but will change for the next month. Secondly, all new recruits to the cohort are assumed to have the same length, s_0. These assumptions can be relaxed, but at the cost of appreciable complication in the computer program.

Below, the present section outlines the general operation of the computer program, section 2 describes the setup of the input data cards, section 3 is an example of a specific application of the program, and Appendix C is a printout of the program.

The computer program is divided into a MAIN PROGRAM and a subroutine, SUBROUTINE TRAP. The purposes and operation of each of these is discussed in some detail below.

Main Program

The first task of the MAIN PROGRAM is to read in all initial input data and print these out. Only data on later temporal changes in the growth and mortality rates are read in later in the program.

The principal DO-loop in the MAIN PROGRAM is DO-loop 900. In general it is assumed that the cohort can be divided into several subcohorts, each with a different growth rate, G(s,t). The DO-loop 900 sums over all of the subcohorts.

The simulation of each subcohort size distribution through time is performed by DO-loop 700 in the MAIN PROGRAM. Within this DO-loop are two main subloops. The first of these, DO-loop 100, uses Eq. (A.21) to calculate the part of N(s,t) resulting from reproduction during the preceding time interval. Within DO-loop 100, a call is made to SUBROUTINE TRAP to calculate $I(s_0,s)$ and $J(s_0,s)$. The second loop, DO-loop 500, calculates $N(s,t)$ resulting from an initial size distribution at the beginning of the preceding time period using Eq. (A.42). Within DO-loop 500 is a main subloop, DO-loop 450, which calculates $R\{t_i + I(s), t + I(s)\}$ (see Eq. A.41).

Values of the size distribution, $N(s,t)$, through time are stored in the array SDIST(I,J), and then printed out near the end of the MAIN PROGRAM.

Subroutine Trap

SUBROUTINE TRAP is called from DO-loop 100 of the MAIN PROGRAM. It calculates $I(s_0,s)$ and $J(s_0,s)$ for every value of s. The trapezoidal method is used in evaluating the integrals. These integrals are used in DO-loop 100 to evaluate Eq. (A-21). The values of $I(s_0,s)$ from s_0 to s are stored and then later inverted numerically in DO-loop 500 to obtain s in terms of values of $I(s_0,s)$. This yields the function $s = F\{I(s_0,s)\}$. Later in DO-loop 500, the values $t_i - t + I(s_0,s)$ are used as the argument of F, to give $F\{t_i - t + I(s_0,s)\}$ (see Eq. A.42). Then a linear interpolation technique is used to compute $N_i(F\{t_i - t + I(s_0 s,)\})$, which is necessary in evaluating Eq. (A.42).

2. Input data

Card A

Input parameters: NSIZES, NSIZEC, NBIRTH, NCHNGE, NRUNTM, NII, NIII, NGROW

Format: 8I5

NSIZES = Number of size classes into which the cohort is divided.

NSIZEC = Number of sizes at which input data on size-dependent mortality and growth rates are given.

NBIRTH = Number of time intervals during the spawning period at which the instantaneous numbers spawned per month are given. If there is no reproduction, set NBIRTH = 0.

NCHNGE = Number of times during the projected course of the simulation at which the mortality and growth rates change. Since these quantities are usually assumed to change month-to-month, NCHNGE is a measure of the number of months in the projected simulation.

NRUNTM = Number of time steps in the simulation.

NII, NIII = These integers control the printing out of detailed information on the computations, which may be useful for diagnostic purposes. For example, if we set NII = 6, certain computational details will be printed out every time the index I in DO-loop 700 is a multiple of six. For other values of I, the WRITE statements are skipped. The other integer, NIII, controls other WRITE statements. To understand and utilize these computational printouts, the program users will have to familiarize themselves with the details of the program.

NGROW = Number of subcohorts having different growth rates.

Card B

Input parameter: TO

Format: 2E10.0

TO = Time of the beginning of the simulation

Card C

Input parameters: DELSIZ, DELCLA, DELSZA

Format: 4E10.0

DELSIZ = Length of size classes into which the cohort is divided. It seems best to make DELSIZ as small as practical for more accuracy.

DELCLA = Length of size intervals between which mortality and growth rate data as functions of size are given.

DELSZA = Length of desired size-class printout; obtained by summing over groups of size classes of width DELSIZ. For example, DELSIZ may be equal to 0.5 millimeters, but if the user wants to print out results of N(s,t) for 5.0 millimeter, then the user must set DELSZA = 5.0.

Card D

Input parameter: SIZE(1)

Format: E10.0

SIZE(1) = Size at time of reproduction of cohort members.

Card E

Input parameters: ZNA(I), I=1, NSIZEC

Format: 7E10.0

ZNA(I) = Size-specific natural mortality for size class I.

Cards F

Input parameters: ZIA(I), I=1,NSIZEC

Format: 7E10.0

ZIA(I) = Size-specific impingement mortality for size class I.

Cards G

Input parameters: GA(I), I=1,NSIZEC

Format: 7E10.0

GA(1) = Size-specific growth rate for size class I.

Cards H

Input parameters: BA(I), I=1,NBIRTH

Format: 7E10.0

BA(I) = Instantaneous reproduction rate (numbers per month, for example) through time during the spawning period. If there is no reproduction, leave one blank card here.

Cards I

Input parameters: TBRT(I), I=1,NBIRTH

Format: 7E10.0

TBERT(I) = Times during the spawning period at which numbers spawned per unit time (e.g., month) are given. If there is no reproduction, leave one blank card here.

Cards J

Input parameters: TIMEA(I), I=2,NCHNGE

Format: 7E10.0

TIMEA(I) = Times during the projected simulation run at which the growth and mortality rates are changed. TIMEA(1) is automatically set to 0.0.

Cards K

Input parameters: TIMEPL(I), I=1,NRUNTM

Format: 7E10.0

TIMEPL(I) = Times at which the size distribution is computed and printed out. It is necessary to at least have one value of TIMEPL(I) paired to each value of TIMEA(I). Actually it is best to set TIMEPL(I) to a value very slightly smaller (say a fraction of a day) than the paired value of TIMEA(I).

Card L

Input parameter: DENDPA

Format: E10.0

DENDPA = Coefficient of effects of total population number on the growth rate (ρ in Eq. 75).

Cards M

Input parameters: FRACA(I), I=1,NGROW

Format: 7E10.0

FRACA(I) = Constant setting growth rate of subcohort I. GA(J) = FRACA(I)* GAA(J) is the growth rate of subcohort I at size J.

Cards N

Input parameters: FRACB(I), I=1,NGROW

Format: 7E10.0

FRACB(I) = Fraction of the total cohort in subcohort I.

Card O

Input parameters: NINIT, NUINT

Format: 2I5

NINIT: If NINIT = 1, there is an initial size distribution at time t = TO; otherwise all the size classes initially have zero population.

NUINT: The first NUINT size classes are assigned initial values greater than or equal to zero.

Cards P

Input parameters: SNUMIN(I), I=1,NUINT

Format: 7E10.0

SNUMIN = Initial population (t = TO) at size class I

Card Sets Q, R, S

A new sequence of these three sets is read in every time the current time, T, exceeds the next value of TIMEA(I).

Cards Q

Input parameters: ZNA(I), I=1,NSIZEC

Format: 7E10.0

ZNA(I) = Size-specific natural natural mortality for size class I.

Cards R

Input parameters: ZIA(I), I=1,NSIZEC

Format: 7E10.0

ZIA(I) = Size-dependent impingement mortality for size class I.

Cards S

Input parameters: GA(I), I=1,NSIZEC

Format: 7E10.0

GA(I) = Size-specific growth rate for size class I.

3. Example application of the program

As an example showing how to set up input data for the computer program, let us consider measurements of larval crappie in an arm of Pickwick Reservoir on the Tennessee River in 1976 (TVA 1976, Hackney and Webb 1977, DeAngelis et al. 1979).

The basic information read as input data is shown in Table 1. It includes the numbers of new recruits (per 1000 cubic meters) into the 5.0 millimeter length class as a function of time in months (Cards H and I). Data on growth rates and natural mortality rates as functions of length are also assumed known (Cards E and G), and are assumed to be constant through time, so NCHNGE = 2 and TIMEA(2) = a very large number. No initial length distribution is assumed, so NININT = 0 (Card M) and no number density-dependence of growth rate is assumed, so DENDPA = 0.0 (Card L). The size of the length classes, DELSIZ, is set at 0.5 millimeters (Card C). The length distribution simulation is to be printed out 20 times at the specified values of TIMEPL(I) (Cards K). No density-dependence is assumed in the growth rate (Card L), and only one subcohort (the whole cohort) is assumed (Card M and Card N).

The input data are printed out by the program as shown in Table 2.

Selected results are shown in Tables 3, 4, and 5. Table 3 shows the numbers of larvae per 1000 cubic meters in the first 10 0.5-millimeter length classes (out of the 200 length classes actually printed out by the program) for all 21 times. Table 4 shows the numbers in the first 10 5.0 millimeter length classes (of the 20 actually printed out by the program) at all times. Finally, Table 5 shows the total population at all times.

```
 200  10   20   3    20   20   20    1                                A
 0.0                                                                  B
 0.5     40.       5.0                                                C
 5.0                                                                  D
 2.1      2.1       2.1       2.1       2.1       2.1       2.1       E
 2.1      2.1       2.1                                               E
 0.0      0.0       0.0       0.0       0.0       0.0       0.0       F
 0.0      0.0       0.0                                               F
 5.45    54.0      95.0      10.9      10.9      10.9      10.9       G
10.9     10.9      10.9      10.9      10.9                           G
 0.0      2.5       3.75      0.0      50.      250.      187.5       H
 0.0      0.0       0.0       0.0       0.0       0.0       0.0       H
 0.0      0.0       0.0       0.0       0.0       0.0                 H
 0.0      0.25      0.50      0.75      1.0       1.25      1.5       I
 1.75     2.0       2.25       2.5       2.75      3.0       3.25     I
 3.50     3.75      4.00      4.25      4.50      4.75      5.00      I
 100.                                                                 J
 0.0      0.25      0.50      0.75      1.0       1.25      1.5       K
 1.75     2.0       2.25       2.5       2.75      3.0       3.25     K
 3.50     3.75      4.00      4.25      4.50      4.75                K
 0.0                                                                  L
 1.0                                                                  M
 1.0                                                                  N
   0    0                                                             O
```

Table B.1. The input data cards relevant to the example. The meaning of the individual cards is given in section 2.

```
                    PARTIAL DIFFERENTIAL EQUATION MODEL OF A FISH COHORT SIZE DISTRIBUTION

NSIZES= 200    NSILEC=  10    NBIRTH=  20    NCHNGE=   3    SIZE CLASS          MORTALITY RATE      GROWTH RATE

NRUNTH=  20    NII=  20    NIII=  20                         0.50000000E 01     0.20999994E 01      0.54499998E 01
                                                             0.45000000E 02     0.20999994E 01      0.54000000E 02
NINIT=   0    NUINT=    0                                    0.85000000E 02     0.20999994E 01      0.95000000E 02
                                                             0.12500000E 03     0.20999994E 01      0.10900000E 02
                                                             0.16500000E 03     0.20999994E 01      0.10900000E 02
DELSIZ=  0.50000000E 00  DELCLA=  0.40000000E 02             0.20500000E 03     0.20999994E 01      0.10900000E 02
                                                             0.24500000E 03     0.20999994E 01      0.10900000E 02
                                                             0.28500000E 03     0.20999994E 01      0.10900000E 02
DELSZA=      5.0000                                          0.32500000E 03     0.20999994E 01      0.10900000E 02
                                                             0.36500000E 03     0.20999994E 01      0.10900000E 02



                                                                         PARAMETER CHANGES OCCUR AT

                                                             TIMEA=  0.0
                                                             TIMEA=  0.10000000E 03
                                                             TIMEA=  0.0



  TIMES FOR WHICH SIZE DISTRIBUTION IS CALCULATED            TIME                BIRTH RATE

   1   0.0                                                    0.0                0.0
   2   0.25000000E 00                                         0.25000000E 00     0.25000000E 01
   3   0.50000000E 00                                         0.50000000E 00     0.37500000E 01
   4   0.75000000E 00                                         0.75000000E 00     0.0
   5   0.10000000E 01                                         0.10000000E 01     0.50000000E 02
   6   0.12500000E 01                                         0.12500000E 01     0.25000000E 03
   7   0.15000000E 01                                         0.15000000E 01     0.18750000E 03
   8   0.17500000E 01                                         0.17500000E 01     0.0
   9   0.20000000E 01                                         0.20000000E 01     0.0
  10   0.22500000E 01                                         0.22500000E 01     0.0
  11   0.25000000E 01                                         0.25000000E 01     0.0
  12   0.27500000E 01                                         0.27500000E 01     0.0
  13   0.30000000E 01                                         0.30000000E 01     0.0
  14   0.32500000E 01                                         0.32500000E 01     0.0
  15   0.35000000E 01                                         0.35000000E 01     0.0
  16   0.37500000E 01                                         0.37500000E 01     0.0
  17   0.40000000E 01                                         0.40000000E 01     0.0
  18   0.42500000E 01                                         0.42500000E 01     0.0
  19   0.45000000E 01                                         0.45000000E 01     0.0
  20   0.47500000E 01                                         0.47500000E 01     0.0

                                                          DENDPA=  0.0
```

Table B.2. The format in which the input data is printed out by the program.

ESTIMATED SIZE DISTRIBUTIONS

SIZES

TIME	5.0000	5.5000	6.0000	6.5000	7.0000	7.5000	8.0000	8.5000	9.0000	9.5000
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.2500	0.4587	0.2395	0.0867	0.0006	0.0	0.0	0.0	0.0	0.0	0.0
0.5000	0.6881	0.4981	0.3296	0.2225	0.1318	0.0738	0.0303	0.0022	0.0001	0.0
0.7500	0.0	0.2083	0.2993	0.3325	0.2437	0.1855	0.1362	0.1012	0.0708	0.0473
1.0000	9.1743	4.7899	1.7336	0.0120	0.0689	0.1122	0.1362	0.1468	0.1202	0.0969
1.2500	45.8716	26.7261	12.6592	4.4928	2.6369	1.4755	0.6053	0.0443	0.0228	0.0389
1.5000	34.4037	31.8458	26.4571	22.2095	14.1025	8.8742	4.8426	2.1794	1.4225	0.9467
1.7500	0.0	10.4128	14.9671	16.6234	14.4785	13.0159	11.3513	9.9555	7.3607	5.2521
2.0000	0.0	0.0	0.0	0.0	3.4426	5.6120	6.8112	7.3420	6.7179	6.1421
2.2500	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0605	1.9439
2.5000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2.7500	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3.0000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3.2500	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3.5000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3.7500	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4.0000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4.2500	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4.5000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4.7500	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table B.3. Predicted numbers of larvae per 1000 cubic meters in the first eight 0.5 millimeter length classes for twenty time periods.

ESTIMATED SIZE DISTRIBUTIONS

SIZES

TIME	5.0000	10.0000	15.0000	20.0000	25.0000	30.0000	35.0000	40.0000	45.0000	50.0000
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.2500	0.7855	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.5000	1.9765	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.7500	1.6248	0.0508	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1.0000	16.3911	0.3203	0.0014	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1.2500	94.5733	0.4518	0.0867	0.0009	0.0	0.0	0.0	0.0	0.0	0.0
1.5000	147.2839	1.1442	0.1787	0.0480	0.0037	0.0	0.0	0.0	0.0	0.0
1.7500	103.4173	9.9611	0.1066	0.0889	0.0363	0.0000	0.0	0.0	0.0	0.0
2.0000	36.0678	29.9345	1.8343	0.0463	0.0491	0.0106	0.0008	0.0000	0.0	0.0
2.2500	3.0044	26.8748	9.5982	1.0238	0.0782	0.0288	0.0145	0.0059	0.0013	0.0000
2.5000	0.0	6.4241	11.5279	5.1141	0.9855	0.0194	0.0215	0.0141	0.0087	0.0050
2.7500	0.0	0.0	3.8952	5.3876	3.4136	0.2114	0.0177	0.0078	0.0102	0.0087
3.0000	0.0	0.0	0.0037	1.4140	2.5960	1.3156	0.3429	0.1186	0.0264	0.0027
3.2500	0.0	0.0	0.0	0.0	0.2150	2.0872	1.4176	0.6963	0.2653	0.1032
3.5000	0.0	0.0	0.0	0.0	0.0	0.9713	1.1481	0.9630	0.7719	0.5226
3.7500	0.0	0.0	0.0	0.0	0.0	0.0002	0.1131	0.3890	0.5157	0.4951
4.0000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0093	0.0931
4.2500	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4.5000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4.7500	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table B.4. Predicted numbers of larvae per 1000 cubic meters in the first eight 5.0 millimeter length classes for twenty time periods.

```
TIME=    0.0        TOTAL  POPULATION=        0.0
TIME=    0.2500     TOTAL  POPULATION=        0.7855
TIME=    0.5000     TOTAL  POPULATION=        1.9765
TIME=    0.7500     TOTAL  POPULATION=        1.6756
TIME=    1.0000     TOTAL  POPULATION=       16.7127
TIME=    1.2500     TOTAL  POPULATION=       95.1125
TIME=    1.5000     TOTAL  POPULATION=      148.6581
TIME=    1.7500     TOTAL  POPULATION=      113.6211
TIME=    2.0000     TOTAL  POPULATION=       67.9819
TIME=    2.2500     TOTAL  POPULATION=       40.6507
TIME=    2.5000     TOTAL  POPULATION=       24.3228
TIME=    2.7500     TOTAL  POPULATION=       14.5276
TIME=    3.0000     TOTAL  POPULATION=        8.6641
TIME=    3.2500     TOTAL  POPULATION=        5.1604
TIME=    3.5000     TOTAL  POPULATION=        3.0725
TIME=    3.7500     TOTAL  POPULATION=        1.7931
TIME=    4.0000     TOTAL  POPULATION=        0.8475
TIME=    4.2500     TOTAL  POPULATION=        0.2036
TIME=    4.5000     TOTAL  POPULATION=        0.0012
TIME=    4.7500     TOTAL  POPULATION=        0.0
```

Table B.5. Predicted total population numbers per 1000 cubic meters for twenty time periods.

APPENDIX C: THE COMPUTER PROGRAM

```
      IMPLICIT REAL*4(A-H,O-Z)
      COMMON SMAX,G
      COMMON/RATEBK/GA(100), ZA(100), SIZECL(100), DELCLA
      COMMON/SIBLOK/DELSIZ
      DIMENSION TIMEPL(40)
      DIMENSION SZNUMG(500), SDISTG(40,500)
      DIMENSION SZNUMA(500)
      DIMENSION X(500)
      DIMENSION TBRT(50), BA(100)
      DIMENSION TIMEA(30), SZNNEW(500)
      DIMENSION GAA(100), FRACA(20), FRACB(20)
      DIMENSION SDISTQ(40,500)
      DIMENSION SDISTP(40,20)
      COMMON/TEGIBK/TEGI(501), SA(501)
      COMMON/SIZEBK/SIZE(501)
      DIMENSION ZIA(100), ZMA(100), SDISTH(40,20)
      DIMENSION SNUMIN(500)
C
C
C --- THIS PROGRAM SOLVES A PARTIAL DIFFERENTIAL EQUATION MODEL FOR THE
C --- SIZE DISTRIBUTION, N(S,T), OF A FISH COHORT FROM THE TIME IT IS
C --- SPAWNED (OR RECRUITED INTO A GIVEN SPECIFIED SIZE CLASS).  THE
C --- MORTALITY RATE, ZA(S,T), AND THE GROWTH RATE, GA(S,T),
C --- ARE BOTH CONSIDERED TO BE FUNCTIONS OF SIZE, S, AND TIME, T, IN GENERAL.
C --- THE PARAMETERS ZA(S,T) AND GA(S,T) ARE READ IN AS NUMERICAL DATA
C --- TO THE PROGRAM.
C
C --- THE BASIC TIME SCALE OF THE MODEL IS THE MONTH.  T - 0.0 CORRESPONDS
C --- TO THE START OF THE SPAWNING PERIOD, T = 1.0 TO A MONTH LATER, ETC.
C
C
C
C --- READ PARAMETER VALUES
C
C --- NSIZES --- NUMBER OF SIZE CLASSES
C --- NRUNTM --- NUMBER OF TIME STEPS
C --- NBIRTH --- NUMBER OF TIME INTERVALS DURING SPAWNING SEASON AT WHICH
```

```
C ---              NUMBERS SPAWNED (OR RECRUITED INTO A SPECIFIED SIZE
C ---              CLASS) ARE GIVEN
C --- NSIZEC ---   NUMBER OF INPUT SIZE CLASS DATA FOR ZA(S,T) AND GA(S,T)
C --- NCHNGE ---   NUMBER OF TIMES AT WHICH ZA(S,T) AND GA(S,T) CHANGE OVER THE
C ---              PROJECTED SIMULATION RUN
C --- DELCLA ---   LENGTH OF SIZE CLASSES FOR WHICH MORTALITY, ZA(S,T), AND
C ---              GROWTH RATE, GA(S,T), ARE GIVEN AS INPUT DATA
C --- DELRUN ---   LENGTH OF TIME STEP
C --- DELSIZ ---   LENGTH OF SIZE CLASSES IN SIMULATION RUN
C --- DELSZA ---   LENGTH OF DESIRED SIZE CLASS PRINTOUT
C --- TO -------   INITIAL TIME
C --- TMAX -----   END OF REPRODUCTIVE PERIOD
C --- TBRT(I) --   TIMES DURING SPAWNING PERIOD AT WHICH NUMBERS SPAWNED
C ---              (OR RECRUITED INTO A GIVEN SPECIDIED SIZE CLASS) PER
C ---              UNIT TIME (MONTH), BA(I), ARE GIVEN
C --- TIMEA(I) -   TIMES AT WHICH ZA(S,T) AND G(S,T) VALUES ARE CHANGED (NORMALLY
C ---              EACH MONTH
C --- TIMEPL(I) -  TIMES FOR WHICH SIZE DISTRIBUTION IS CALCULATED
C --- SIZECL(I) -  SIZE CLASSES FOR WHICH INPUT DATA ZA(S,T) AND GA (S,T)
C ---              ARE GIVEN
C --- SIZE(1) --   SIZE AT BIRTH
C --- SIZE(I) --   AVERAGE LENGTH OF AN INDIVIDUAL IN SIZE CLASS I
C --- ZNA(I) ---   SIZE-SPECIFIC NATURAL MORTALITY RATE IN SIZE CLASS I
C --- ZIA(I) ---   SIZE-SPECIFIC IMPINGEMENT MORTALITY RATE IN SIZE CLASS I
C --- ZA(I) ----   SIZE-SPECIFIC MORTALITY RATE FOR SIZE CLASS I
C --- GA(I) ----   SIZE-SPECIFIC GROWTH RATES
C --- BA(I) ----   REPRODUCTION RATE DURING SPAWNING PERIOD (NUMBERS/MONTH)
C --- NII ------   THE INTEGER CONTROLS THE PRINTING OUT OF DETAILED COMPUTATIONS
C ---              AT GIVEN TIME STEPS.  FOR EXAMPLE, IF WE SET NII = 10, MANY
C ---              COMPUTATIONAL DETAILS WILL BE PRINTED OUT EVERY TIME THE
C ---              INDEX I IN DO-LOOP 700 IS A MULTIPLE OF SIX.
C --- NIII -----   THE INTEGER CONTROLS THE PRINTING OUT OF DETEILED COMPUTATIONS
C --- NUINT ----   NUMBER OF INITIAL SIZE DISTRIBUTION POINTS
C --- NINIT ----   IF NINIT = 1, THERE IS AN INITIAL SIZE DISTRIBUTION
C --- SNUMIN(I) -  INITIAL NUMBER OF FISH IN SIZE CLASS I
C --- DENDPA ---   COEFFICIENT OF EFFECTS OF NUMBER DENSITY ON GROWTH RATE
C --- NGROW ----   NUMBER OF SUBCOHORTS HAVING DIFFERENT GROWTH RATES
C --- FRACA(I) -   FRACA(LI)*GAA(J) IS THE GROWTH RATE OF SUBCOHORT LI AT SIZE J
C --- FRACB(I) -   FRACB(LI)*SNUMIN(J) IS THE INITIAL POPULATION OF SUBCOHORT LI
C ---              IN SIZE CLASS J
```

```
C
C
      READ(5,1000) NSIZES, NSIZEC, NBIRTH, NCHNGE, NRUNTM, NII, NIII
     1,NGROW
 1000 FORMAT(14I5)
      READ(5,1001) TO
 1001 FORMAT(7E10.0)
      READ(5,1001) DELSIZ, DELCLA, DELSZA
      READ(5,1001) SIZE(1)
      READ(5,1001) (ZNA(I),I=1,NSIZEC)
      READ(5,1001) (ZIA(I),I=1,NSIZEC)
      READ(5,1001) (GA(I),I=1,NSIZEC)
      IF(NBIRTH .EQ. 0) GO TO 2
      READ(5,1001) (BA(I),I=1,NBIRTH)
      READ(5,1001) (TBRT(I),I=1,NBIRTH)
    2 CONTINUE
      TIMEA(1) = 0.0
      READ(5,1001) (TIMEA(I),I=2,NCHNGE)
      READ(5,1001) (TIMEPL(I),I=1,NRUNTM)
      READ(5,1001) DENDPA
      READ(5,1001) (FRACA(I),I=1,NGROW)
      READ(5,1001) (FRACB(I),I=1,NGROW)
      DO 3 I=1,500
      SNUMIN(I) = 0.0
      SZNUMG(I) = 0.0
      DO 3 J=1,40
      SDISTQ(J,I) = 0.0
    3 CONTINUE
      READ(5,1000) NINIT, NUINT
      IF(NINIT .EQ. 0) GO TO 7
      READ(5,1001) (SNUMIN(I), I=1,NUINT)
    7 CONTINUE
      DO 10 I=1,NSIZEC
      ZA(I) = ZNA(I) + ZIA(I)
      GAA(I) = GA(I)
   10 CONTINUE
      TBRT(1) = TO
      SIZECL(1) = SIZE(1)
      DO 18 I=1,NSIZEC
      SIZECL(I+1) = SIZECL(I) + DELCLA
   18 CONTINUE
      WRITE(6,2000)
 2000 FORMAT(1H1,20X,'PARTIAL DIFFERENTIAL EQUATION MODEL OF A FISH COHO
     1RT SIZE DISTRIBUTION',////)
      WRITE(6,2006) NSIZES, NSIZEC, NBIRTH, NCHNGE
 2006 FORMAT(1H ,5X,'NSIZES=',I4,4X,'NSIZEC=',I4,4X,'NBIRTH=',I4,4X,
     1'NCHNGE=',I4,//)
      WRITE(6,2016) NRUNTM,NII, NIII
 2016 FORMAT(1H ,5X,'NRUNTM=',I4,4X,'NII=',I4,4X,'NIII=',I4,//)
      WRITE(6,2017) NINIT, NUINT
 2017 FORMAT(1H ,5X,'NINIT=',I4,4X,'NUINT=',I4,//)
      WRITE(6,2007) DELSIZ, DELCLA
 2007 FORMAT(1H ,5X,'DELSIZ= ',E15.8,2X,'DELCLA= ',E15.8,//)
      WRITE(6,2009) DELSZA
 2009 FORMAT(1H ,5X,'DELSZA= ',F10.4,//)
      WRITE(6,2014)
 2014 FORMAT(1H ,///,10X,'TIMES FOR WHICH SIZE DISTRIBUTION IS CALCULATE
     1D',//)
      DO 16 I=1,NRUNTM
      WRITE(6,2099) I,TIMEPL(I)
   16 CONTINUE
      WRITE(6,2004)
      WRITE(6,2001)
 2001 FORMAT(////,5X,'SIZE CLASS',10X,'MORTALITY RATE',6X,'GROWTH RATE',
     1//)
      DO 20 I=1,NSIZES
      SIZE(I+1) = SIZE(I) + DELSIZ
   20 CONTINUE
      DO 30 I=1,NSIZEC
      WRITE(6,2002) SIZECL(I), ZA(I), GA(I)
 2002 FORMAT(1H ,5X,6(E15.8,3X))
   30 CONTINUE
      WRITE(6,2011)
 2011 FORMAT(1H ,////,20X,'PARAMETER CHANGES OCCUR AT',//)
      DO 35 I=1,NCHNGE
      WRITE(6,2012) TIMEA(I)
 2012 FORMAT(1H ,5X,'TIMEA= ',E15.8)
   35 CONTINUE
      WRITE(6,2003)
 2003 FORMAT(////,5X,'TIME',16X,'BIRTH RATE',//)
```

```
      DO 40 I=1,NBIRTH
      WRITE(6,2002) TBRT(I), BA(I)
   40 CONTINUE
      WRITE(6,2008) DENDPA
 2008 FORMAT(1H ,/,5X,'DENDPA= ',E15.8,//)
      MSIZE = DELSZA/DELSIZ
      LSIZES = NSIZES/MSIZE
      WRITE(6,2013) MSIZE, LSIZES
 2013 FORMAT(1H ,///,5X,'MSIZE= ',I5,5X,'LSIZES= ',I5,//)
      DO 45 I=1,40
      DO 45 L=1,20
      SDISTP(I,L) = 0.0
      SDISTH(I,L) = 0.0
   45 CONTINUE
      WRITE(6,2022) NGROW
 2022 FORMAT(1H ,5X,'NUMBER OF SUBCOHORTS, NGROW= ',I5,//)
      WRITE(6,2023)  (FRACA(I),I=1,NGROW)
      WRITE(6,2024)  (FRACB(I),I=1,NGROW)
 2023 FORMAT(1H ,5X,'FRACA= ',14(F7.3,1X))
 2024 FORMAT(1H ,5X,'FRACB= ',14(F7.3,1X))
C
C --- CALCULATE THE ANALYTICAL SOLUTION
C --- ITERATE MODEL OVER TIME
C
      DO 900 LI=1,NGROW
      DO 43 I=1,NSIZES
      SDISTG(1,I) = 0.0
   43 CONTINUE
      JTIME = 0
      T = TO
      TLAST = TO
      JLAST = 1
      NRUNTP = NRUNTM + 1
      TMAX = TBRT(NBIRTH)
      DO 700 I=1,NRUNTM
      T = TIMEPL(I)
      STOREI = 0.0
      TEGI(1) = STOREI
      STOREJ = 0.0
 2045 FORMAT(1H ,5X,'I= ',I5)
```

```
      DO 46 J=1,NCHNGE
      IF(T .LE. TIMEA(J+1))  GO TO 47
   46 CONTINUE
   47 CONTINUE
      JTIME = J
      TI = TIMEA(JTIME)
      DO 50 J=1,NSIZES
      IF(I .EQ. 1)  GO TO 49
      SZNUMG(J) = 0.0
   49 CONTINUE
      SZNNEW(J) = 0.0
   50 CONTINUE
      DO 51 J=1,NSIZEC
      GA(J) = FRACA(LI)*GAA(J)
   51 CONTINUE
      IF(T .GE. TMAX)  GO TO 60
      DO 55 J=1,NBIRTH
      IF(TBRT(J)  .LE.  T)  GO TO 55
      GO TO 56
   55 CONTINUE
      GO TO 60
   56 CONTINUE
      BIRTH = BA(J-1)  +  ((T-TBRT(J-1))/DELBIR)*(BA(J)  -  BA(J-1))
      GO TO 61
   60 CONTINUE
      BIRTH = 0.0
   61 CONTINUE
      GMIN = GA(1)
      SZNNEW(1)  =  BIRTH/GMIN
      IF(I .NE.  (I/NII)*NII)  GO TO 63
      WRITE(6,2004)
 2004 FORMAT(1H1)
   63 CONTINUE
C
C
C --- CALCULATION OF PORTION OF N(S,T)  RESULTING FROM REPRODUCTION IN
C     THE TIME INTERVAL
C
      DO 100 J=2,NSIZES
      CALL TRAP(SIZE(J-1),DELSIZ,8,1.,FACTRI,GNV)
      FACTRI = FACTRI + STOREI
      STOREI = FACTRI
      TEGI(J) = STOREI
      TB = T - FACTRI
      CALL TRAP(SIZE(J-1),DELSIZ,8,0.,FACTRJ,GNV)
      IF(I .NE. (I/NIII)*NIII) GO TO 69
      WRITE(6,2099) J,SIZE(J-1),DELSIZ,FACTRI,GNV,STOREJ,TB
 2099 FORMAT(1H ,5X,I5,2X,6(E15.8,1X))
   69 CONTINUE
      FACTRJ = FACTRJ + STOREJ
      STOREJ = FACTRJ
      IF(I .NE. (I/NII)*NII) GO TO 75
      WRITE(6,2005) I,J,FACTRI,FACTRJ
 2005 FORMAT(1H ,5X,I3,2X,I3,2X,'I(S)= ',E15.8,3X,'J(S)= ',E15.8)
   75 CONTINUE
      TLOWER = TLAST
      IF(T .GE. TMAX) GO TO 90
      IF(TB .GT. TMAX .OR. TB .LT. TLOWER) GO TO 90
      DO 80 K=1,NBIRTH
      IF(TBRT(K) .LE. TB) GO TO 80
      GO TO 81
   80 CONTINUE
   81 CONTINUE
      IF(K .EQ. 1) GO TO 90
      BIRTH = BA(K-1) + ((TB-TBRT(K-1))/(TBRT(K)-TBRT(K-1)))*
     1(BA(K) - BA(K-1))
      GO TO 91
   90 CONTINUE
      BIRTH = 0.0
   91 CONTINUE
      IF(I .NE. (I/NII)*NII) GO TO 95
      WRITE(6,2010) TB,BIRTH,GNV,TBRT(K),BA(K)
 2010 FORMAT(1H ,5X,'TB= ',E15.8,2X,'BIRTH= ',E15.8,2X,'GNV= ',E15.8,
     12X,'TBRT= ',E15.8,2X,'BA= ',E15.8)
   95 CONTINUE
      IF(FACTRJ .GT. 30.) FACTRJ = 30.
      SZNNEW(J)= BIRTH*GNV*EXP(-FACTRJ)
  100 CONTINUE
  105 CONTINUE
      IF(I .NE. (I/NIII)*NIII) GO TO 111
      DO 110 J=1,NSIZES
      WRITE(6,2015) SIZE(J), TEGI(J)
 2015 FORMAT(1H ,5X,'SIZE= ',E15.8,2X,'TEGI= ',E15.8)
  110 CONTINUE
  111 CONTINUE
C
C
C
  150 CONTINUE
      DO 155 J=1,NSIZES
      IF(I .EQ. 1) GO TO 153
      SZNUMG(J) = SDISTG(I-1,J)
      GO TO 154
  153 CONTINUE
      SZNUMG(J) = SNUMIN(J)
      SZNUMG(J) = SNUMIN(J)*FRACR(LI)
  154 CONTINUE
      IF(I .NE. (I/NIII)*NIII) GO TO 155
      WRITE(6,2034) J, SZNUMG(J)
 2034 FORMAT(1H ,5X,'J= ',I5,5X,'SZNUMG= ',E15.8)
  155 CONTINUE
  156 CONTINUE
      WRITE(6,2018)
 2018 FORMAT(///)
      IF(JTIME .LE. JLAST) GO TO 175
      READ(5,1001) (ZNA(II),II=1,NSIZEC)
      READ(5,1001) (ZIA(II),II=1,NSIZEC)
      READ(5,1001) (GA(II),II=1,NSIZEC)
      WRITE(6,2019) T
 2019 FORMAT(/,5X,'CHANGE IN GROWTH AND MORTALITY RATES AT TIME T = ',
     1F10.4,/)
      WRITE(6,2001)
      DO 180 II=1,NSIZEC
      ZA(II) = ZNA(II) + ZIA(II)
      WRITE(6,2002) SIZECL(II), ZA(II), GA(II)
  180 CONTINUE
      WRITE(6,2066) I,JTIME,JLAST,T
 2066 FORMAT(1H ,//,5X,3I5,4(E15.8,2X))
  175 CONTINUE
C
```

```
C --- CALCULATION OF THAT PORTION OF N(S,T) RESULTING FROM INDIVIDUALS
C     ALREADY PRESENT AT THE START OF THE INTERVAL
C
      IF(I .NE. (I/NIII)*NIII) GO TO 339
      WRITE(6,2097)
 2097 FORMAT(1H ,5X,'IN T .GT. TIMEA(I)',/)
  339 CONTINUE
      DO 500 J=1,NSIZES
      ARG = TEGI(J) + TLAST - T
      IF(ARG .LE. TEGI(1)) GO TO 499
      DO 350 K=1,500
      IF(ARG .GT. TEGI(K)) GO TO 350
      GO TO 351
  350 CONTINUE
  351 CONTINUE
      SUBS = SIZE(K-1) + ((ARG-TEGI(K-1))/(TEGI(K)-TEGI(K-1)))*(SIZE(K)
     1 - SIZE(K-1))
      IF(I .NE. (I/NII)*NII) GO TO 395
      WRITE(6,2032) J,K,T
 2032 FORMAT(1H ,2X,2I5,F10.5)
  395 CONTINUE
      DO 400 K=1,500
      IF(SUBS .GT. SIZE(K)) GO TO 400
      GO TO 401
  400 CONTINUE
  401 CONTINUE
      FACTRA = SZNUMG(K-1) + ((SUBS-SIZE(K-1))/DELSIZ)*
     1(SZNUMG(K) - SZNUMG(K-1))
      IF(FACTRA .LE. 0.0) FACTRA = 0.0
      DO 407 K=1,50
      IF(SUBS .GT. SIZECL(K)) GO TO 407
      GO TO 406
  407 CONTINUE
  406 CONTINUE
      G = GA(K-1) + ((SUBS-SIZECL(K-1))/DELCLA)*(GA(K)-GA(K-1))
      DO 412 K=1,50
      IF(SIZE(J) .GT. SIZECL(K)) GO TO 412
      GO TO 413
  412 CONTINUE
  413 CONTINUE
```

```
      GD = GA(K-1) + ((SIZE(J) - SIZECL(K-1))/DELCLA)*(GA(K)-GA(K-1))
      IF(I .NE. (I/NII)*NII) GO TO 415
      WRITE(6,2033) ARG,TEGI(J),TEGI(K),SUBS,FACTRA,G
 2033 FORMAT(1H ,4X,'ARG= ',E15.8,1X,'TEGJ= ',E15.8,1X,'TEGK= ',E15.8,
     11X,'SA= ',E15.8,'FACTRA= ',E15.8,1X,'G= ',E15.8)
  415 CONTINUE
      GNV = 1./G
C
C --- CALCULATION OF THE INTEGRAL R(TI,T)
C --- SEE EQUATION (44) IN TEXT
C
      TOTT = TIMEPL(I) - TIMEPL(I-1)
      JTEND = 50
      DJTEND = JTEND
      DELTAU = TOTT/DJTEND
      TAU = TLAST + TEGI(J)
      TAUTEG = 0.0
      DO 450 JT=1,JTEND
      ARG = TAU - T
      IF(ARG .LT. TEGI(1)) GO TO 449
      DO 430 K=1,100
      IF(ARG .GT. TEGI(K)) GO TO 430
      GO TO 431
  430 CONTINUE
  431 CONTINUE
      SUBS = SIZE(K-1) + ((ARG-TEGI(K-1))/(TEGI(K)-TEGI(K-1)))*(SIZE(K)
     1 - SIZE(K-1))
      DO 440 K=1,100
      IF(SUBS .GT. SIZECL(K)) GO TO 440
      GO TO 441
  440 CONTINUE
  441 CONTINUE
      Z = ZA(K-1) + ((SUBS-SIZECL(K-1))/DELCLA)*(ZA(K) - ZA(K-1))
      DG = (GA(K) - GA(K-1))/DELCLA
      DELL = 1.0
      IF(JT .EQ. 1 .OR. JT .EQ. NSIZES) DELL = 0.5
      TAUTEG = TAUTEG + DELL*DELTAU*Z
  449 CONTINUE
      TAU = TAU + DELTAU
  450 CONTINUE
```

```
C
C
      FACTRJ = TAUTEG
      IF(FACTRJ .GT. 30.) FACTRJ = 30.
      SZNNEW(J) = SZNNEW(J) + FACTRA*EXP(-FACTRJ)*(G/GD)
      IF(I .NE. (I/NII)*NII) GO TO 455
      WRITE(6,2030) I,J, FACTRJ,SZNNEW(J)
 2030 FORMAT(1H ,2X,2I5,5X,'FACTRJ= ',E15.8,2X,'SZNNEW(J)= ',E15.8)
  455 CONTINUE
      GO TO 500
  499 CONTINUE
      SZNNEW(J) = SZNNEW(J)
  500 CONTINUE
C
C
      DO 550 J=1,NSIZES
      SZNUMG(J) = SZNNEW(J)
  550 CONTINUE
  650 CONTINUE
  685 CONTINUE
      TOTAL = 0.0
      DO 690 J=1,NSIZES
      SDISTG(I,J) = SZNUMG(J)
      TOTAL = TOTAL + SDISTG(I,J)
      LL = 1 + ((J-1)/MSIZE)
      SDISTH(I,LL) = SDISTH(I,LL) + SDISTG(I,J)
      IF(I .NE. (I/NII)*NII) GO TO 688
      WRITE(6,2020) I,J,SDISTG(I,J)
 2020 FORMAT(1H ,5X,2I5,5X,5(E15.8,2X))
  688 CONTINUE
  689 CONTINUE
  690 CONTINUE
      TLAST = T
      JLAST = JTIME
  700 CONTINUE
C
C --- OUTPUT RESULTS
C
      IF(LI .NE. 4*(LI/4)) GO TO 851
      NSIZMX = SIZE(NSIZES)
      T = TIMEPL(K)
      WRITE(6,4102) T,(SDISTH(K,I),I=NM,NV)
  870 CONTINUE
      IF(NV .LT. LSIZES) GO TO 860
      DO 895 I=1,NRUNTM
      DO 880 J=1,NSIZES
      SDISTQ(I,J) = SDISTQ(I,J) + SDISTG(I,J)
      SIZE(J+1) = SIZE(J) + DELSIZ
  880 CONTINUE
      DO 890 J=1,LSIZES
      SDISTP(I,J) = SDISTP(I,J) + SDISTH(I,J)
  890 CONTINUE
  895 CONTINUE
  900 CONTINUE
      NV = 0
  950 NM = NV + 1
      NV = NM + 9
      T = 0.0
      IF(NV .GT. NSIZES) NV = NSIZES
      WRITE(6,4104)
      WRITE(6,4103) (SIZE(I),I=NM,NV)
      DO 960 K=1,NRUNTM
      T = TIMEPL(K)
      WRITE(6,4102) T,(SDISTQ(K,I),I=NM,NV)
  960 CONTINUE
      IF(NV .LT. NSIZES) GO TO 950
      DO 975 L=1,LSIZES
      SIZE(L+1) = SIZE(L) + DELSZA
  975 CONTINUE
      NV = 0
  970 NM = NV + 1
      NV = NM + 9
      T = 0.0
      IF(NV .GT. LSIZES) NV = LSIZES
      WRITE(6,4104)
      WRITE(6,4103) (SIZE(I),I=NM,NV)
      DO 980 K=1,NRUNTM
      T = TIMEPL(K)
      WRITE(6,4102) T, (SDISTP(K,I),I=NM,NV)
  980 CONTINUE
```

```
           NRUNT = NRUNTM - 1
           NV = 0
       800 NM = NV + 1
           NV = NM +9
           T = 0.0000
           IF ( NV.GT.NSIZES) NV = NSIZES
           WRITE(6,4104)
      4104 FORMAT(1H1,43X,'ESTIMATED SIZE DISTRIBUTIONS',//,57X,'SIZES',//)
           WRITE(6,4103)  (SIZE(I),I=NM,NV)
      4103 FORMAT(1H ,7X,'TIME',10(F11.4))
           DO 810 K=1,NRUNTM
           T = TIMEPL(K)
                WRITE(6,4102) T,(SDISTG(K,I),I=NM,NV)
      4102 FORMAT(1H ,11(F11.4))
       810 CONTINUE
           IF(NV .LT. NSIZES) GO TO 800
           T = 0.0
           WRITE(6,2004)
           DO 850 K=1,NRUNTM
                TOTAL = 0.0
           DO 840 L=1,NSIZES
                     TOTAL = TOTAL + SDISTG(K,L)
       840 CONTINUE
           T = TIMEPL(K)
           WRITE(6,2021) T, TOTAL
      2021 FORMAT(1H ,5X,'TIME= ',F8.4,4X,'TOTAL POPULATION= ',F11.4)
       850 CONTINUE
       851 CONTINUE
     C
           DO 855 L=1,LSIZES
           SIZE(L+1) = SIZE(L) + DELSZA
       855 CONTINUE
           NV = 0
       860 NM = NV + 1
           NV = NM + 9
           T = 0.0
           IF(NV .GT. LSIZES) NV = LSIZES
           WRITE(6,4104)
           WRITE(6,4103)  (SIZE(I),I=NM,NV)
           DO 870 K=1,NRUNTM
      IF(NV .LT. LSIZES) GO TO 970
      STOP
      END
      SUBROUTINE TRAP(SI,DS,M,X,F,GNV)
C
C --- TRAPEZOID METHOD IS USED TO EVALUATE THE
C --- INTEGRALS I(S)  (X=1)  AND J(S)  (X=0).
C
C --- SUBROUTINE TRAP --- SAMPLE CALL
C --- CALL TRAP(S,DELS,MORT,STEPS,X,F,GROWTH)
C --- WHERE S = SIZE CLASS
C ---          DELS = LENGTH OF SIZE CLASS
C ---          MORT = SPECIFIC MORTALITY RATE
C ---          STEPS = NO. OF SUBDIVISIONS OVER WHICH THE INTEGRAL IS
C                        APPROXIMATED
C ---          X = 0.  TO INTEGRATE Z/G
C                  1.  TO INTEGRATE 1/G
C ---          F = VALUE OF THE INTEGRAL OVER SIZE CLASS I TO I+1
C ---          GROWTH = 1/GROWTH RATE
C
      COMMON/RATEBK/GA(100), ZA(100), SIZECL(100), DELCLA
      DIMENSION GN(20),S(21)
      COMMON SMAX,V
      S(1) = SI
      H = DS / M
      M2 = M + 1
      DO 200 I=1,M2
      DO 50 J=1,100
      IF(SIZECL(J) .LE. SI)  GO TO 50
      GO TO 51
   50 CONTINUE
   51 CONTINUE
      Z = ZA(J-1)  +  ((SI - SIZECL(J-1))/DELCLA)*(ZA(J)  - ZA(J-1))
      G = GA(J-1)  +  ((SI - SIZECL(J-1))/DELCLA)*(GA(J)  - GA(J-1))
      GN(I) = 1./G
      S(I+1) = S(I)  + H
  200 CONTINUE
      SUM = (GN(1)  + GN(M2))/2.
      DO 250 I=2,M
      SUM = SUM + GN(I)
  250 CONTINUE
      Y = 1.0
      IF(X.EQ.0.)  Y = Z
      F = Y * H * SUM
      GNV = GN(M2)
      RETURN
      END
```